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JOURNAL OF ANATOMY

THE CHROMOSOMES OF *SPHENODON PUNCTATUM*

By R. D. KEENAN, B.Med.Sc. (N.Z.)

From the Anatomical Department of the University of Otago, New Zealand

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I. INTRODUCTION

Previous to the year 1928 there was a remarkable paucity of knowledge concerning the chromosomes of Reptiles. Apart from a few isolated observations, principally by Jordan (5), Painter (10, 11), Dalcq (2) and Thatcher (17), this rich field was almost entirely unexplored. Even more remarkable, however, has been the rapidity with which authoritative information has accumulated during the last three years. The technique introduced by Kenji Nakamura (9) has enabled reptilian chromosomes to be fixed in a manner far superior to that obtained by any of the former methods, and with a clarity of outline which has rendered possible an accurate morphological analysis of the constituents of both the primary and secondary meiotic divisions. With the aid of this technique Nakamura and Matthey have now established the chromosome constitution of representatives of almost all the modern reptilian orders, and the latter has advanced a highly interesting theory concerning the evolution of the chromosomal formula of the Autosauri (Lacertilia). The previous lack of knowledge of reptilian chromosomes is far from being a drawback. For, as pointed out by Matthey (7), it obviates the necessity for exploring a mass of erroneous data based on inadequate methods of fixation—a factor which has so hampered the students of mammalian and avian chromosomes. From this point of view it is significant that the superiority of the figures obtained by the use of the Champy-Nakamura technique has enabled Matthey (7) to criticise and modify not only one of his own former observations on the number of chromosomes in *Vipera aspis* (6), but also the observations of all previous workers in this field.

The interest attaching to cytological studies of *Sphenodon* is, of course, referable to the extremely primitive and generalised characters of this Reptile. Extensive information has now been collected concerning the chromosome condition of the principal orders of Amphibia, Reptilia and Mammalia, and the study of *Sphenodon* was dictated by the hope that it would throw some light on the number and the type of the chromosomes possessed by primitive Vertebrates. The object of the present work, therefore, has been directed towards establishing the number and, as far as possible, the morphology of the chromosomes in this Reptile.

II. MATERIAL AND TECHNIQUE

The imperfections in the present work, which is by no means complete, are mainly due to a lack of suitably fixed material. Several testes of *Sphenodon* had been obtained during the course of a number of years by this Department and these had been fixed by one or other of the ordinary agents in use. My studies were commenced on that tissue. Experience has suggested that the months of October, November and December are probably the best season during which to obtain material. Unfortunately, however, the latter is difficult to obtain even in this country, and an animal taken at the beginning of November, 1930, is the only case in which I have been able to secure material satisfactorily fixed and at a suitable season. Owing to the fact that anaphase and telophase stages were almost entirely lacking in my sections, it has not been possible to follow the history of each spermatogonial chromosome through all the meiotic stages which an accurate determination of the fundamental chromosome number demands. In addition, the material was not suitable for the elucidation of the pre-meiotic phases, and my remarks are limited almost entirely to certain definite observations on the spermatogonia and primary spermatocytes. As a description of the technique used has not, to my knowledge, appeared before in any English publication, I append the details here as they were put at the disposal of this Department by Dr Matthey.

All authorities seem to agree that the use of a general anaesthetic, such as chloroform, for killing the animal leads to unsatisfactory fixation. Cutting off the head is usually advised, but as there were reasons why this should not be done, urethane injected per rectum was used. The testis was removed quickly, cut into small pieces and dropped into the fixing fluid. Some of the pieces were further broken up by teasing with porcupine quills.

The composition of the fixing fluid—a modification of Champy's mixture concentrated 1·5 times as strong as the original—is:

Osmic acid 3 % aq. sol.	...	...	4 parts
Chromic acid 1·5 % aq. sol.		...	8 parts
Potassium bichromate 4·5 % aq. sol.			8 parts

After remaining in this fluid for 24 hours the pieces were placed in small glass tubes about 1 in. in length, closed at one end with strips of organdi, washed in

running water for a further 24 hours and then gradually dehydrated with alcohol. The material was next placed in two baths of cedarwood oil and then two baths of paraffin (52° C.)—one for 12 hours and the second for 2 hours. The sections were cut at a thickness of 10 microns. After removing the paraffin with xylol these were bleached in pure turpentine for from 3 to 6 days, then passed through two baths of xylol and carried down to water. If not bleached enough they may be passed through hydrogen peroxide. They were now placed for 12 hours in a bath containing:

Sat. aq. sol. picric acid	50 parts
Glacial acetic acid ...	50 parts

This bath is used for dissolving cellular inclusions and at the same time to increase the affinity of the chromosomes for dyes. For staining the sections Heidenhain's iron-haematoxylin was used.

The efficacy of the fixing fluid of Champy is considered by Matthey to be due to the absence of acetic acid. He states that the addition of this acid in a concentration as dilute even as $\frac{1}{2}$–1 per cent. considerably diminishes the quality of the fixation.

The results obtained from the use of any particular technique depend largely on the individual, and an appreciation of the quality of the fixation of the chromosomes is obtained only by experience. In this case I had the advantage of observing and comparing the results obtained, both from the old methods and from the new. The superiority of the latter was obvious. In properly fixed material the elements are well separated, well defined and regular in outline and, what is of the first importance, there is no difficulty in distinguishing the smaller elements. On the other hand, in imperfectly fixed material the whole cell and its contents appear shrunken and contracted. The chromosomes give the impression of having been drawn towards each other and towards the centre of the cell. This was the usual condition in material fixed with any of the fluids formerly in use. Thus the recognition of the elements was rendered difficult, not only owing to superposition, but also on account of fusion of the larger and clumping of the smaller individuals. Accordingly, when using such material I was never able to obtain any agreement in my cell counts. The material fixed with Champy-Nakamura presented a most striking difference in appearance, so great, indeed, that it might have been taken from another animal. The separation and superior definition of the elements, particularly in the spermatogonia, was well marked and permitted them to be recognised with facility, so that I at once commenced to obtain consistent agreement in my counts. It must, however, be pointed out that whilst the use of this technique has rendered possible the making of certain definite observations, I have not been able to obtain the remarkably clear figures reproduced by Matthey and Nakamura. Whether this is due to certain intrinsic properties of the tissue or to faulty technique cannot be made clear without the use of fresh material for comparison. I should also like to stress the fact, already pointed

out by both these workers, that the chief difficulty in the technique lies in the staining of the sections after the use of this fixing fluid. Variations in coloration have been very obvious in my sections, and there have been, in addition, variations in the quality of the fixation. In general the peripheral portions of the sections were better fixed and, in particular, better coloured than the central portions, though this was by no means invariable. Thus at times the whole central portion of a section would be found totally uncoloured, and yet isolated cells would be found in such an area well fixed and reasonably well coloured. In very rare cases one obtained the chromosomes stained a dense black and sharply defined on a colourless background. Very commonly—and this feature was noticeable in all stages observed—the chromosomes were densely stained, but at the same time imperfectly fixed and showing a marked tendency to clump. In well-fixed cells the most usual condition was to find the chromosomes appearing as pale grey bodies on a background of much the same colour. Consequently, it has been a striking and at times very troublesome fact that the best fixed cells were often very imperfectly coloured.

Another notable observation has been the frequency with which dividing cells tend to occur in limited and isolated areas. Painter (12) stresses the fact already pointed out by earlier workers, Ebner (1899) and Regaud (1910), that the maturation divisions in Mammals occur in waves or cycles running the length of the tubule. Something comparable seems to occur in *Sphenodon*, as I have almost invariably found the cells undergoing spermatogonial and spermatocyte divisions occurring in clumps. A single clump of dividing cells would stand out prominently in the wall of a tubule, while all the neighbouring tubules showed not the slightest sign of activity.

III. OBSERVATIONS

(*a*) *On spermatogonia*

Gonial cells were by no means numerous in my material, and this has necessitated the examination of a large number of sections. The fixation was in general good, but the coloration extremely variable. The study of the spermatogonia I found the most difficult part of the work. Counting is not easy owing to the fact that there is always some superposition in the figures. This would indicate a very short metaphase period. To overcome this difficulty to some extent, I adopted the following procedure. At the commencement of my study of the spermatogonia, when I began to feel confident that I had well-fixed material, I spent a considerable time thoroughly familiarising myself with the relative sizes and shapes of the chromosomes, and it soon became evident that the individual elements could be grouped in pairs showing—at least in the case of the larger elements—striking differences in size and shape. I have, in addition, always adopted the practice of completing the drawing of a cell before attempting to count, and thus, as Painter (15) has stated, "the count becomes more than the enumeration of black dots and rods, it is really a muster of the chromosomes involving the recognition of most of the chromosome pairs."

In the cells in which the chromosomes are most clearly defined and separated, the number of the elements is always 36. In some cases, it is true, I have obtained apparent counts of 33, 34 and 35, but without exception such cells have presented either an obvious absence of one or more of the smaller elements, or alternatively areas in which the chromosomes were so superimposed that it was impossible to be sure whether one were looking at one or more of them. This latter feature seems to affect more the central than the peripheral portion of the equatorial plate. Sometimes I have obtained cells in which the peripheral elements were perfectly clear, while in the centre of the plate differentiation of the individual elements was impossible, owing to their overlapping and proximity to one another. However, when one obtains really good cells it is surprising how readily with practice the chromosomes can be recognised. The figures, perhaps, give the impression that the recognition of the elements is less easy than is actually the case, but in all of them careful focussing was sufficient to prevent any ambiguity.

Another feature which camera lucida drawings fail to emphasise sufficiently is the variation in the manner of the arrangement of the chromosomes on the equatorial plate at metaphase. The rod-shaped chromosomes, instead of lying in the equatorial plane are often disposed obliquely, making an angle with it, while the V or J-shaped chromosomes are arranged with the plane containing the two arms of the V or J either perpendicular to or at varying degrees of obliquity to the equatorial plane. Thus, although the shapes and sizes of the elements are usually sufficiently characteristic to prevent any confusion in their recognition owing to this oblique arrangement, it so happens that when one traces them with the camera lucida, the V's and J's often appear less flexed and their limbs shorter than is actually the case. This shortening, which may also affect the rods, is, of course, more marked in the case of the larger elements. In making an alignment of the gonial pairs I selected a cell in which this obliquity was at a minimum, and it was at once obvious that the pairs could be drawn up in descending order of magnitude. According to size and shape, the chromosomes can be grouped into four classes:

(1) Six pairs of atelomitic chromosomes which are V or J-shaped.
(2) Eight pairs of telomitic chromosomes which are rod-shaped.
(3) One pair of very short rod-like chromosomes.
(4) Six microchromosomes which are dot-like.

In a general way they are grouped on the equatorial plate with the larger elements surrounding the smaller as is found in other Reptiles.

Atelomitic chromosomes. When the chromosomes are drawn up in serial alignment as in fig. 21, it is obvious that the largest pair of atelomitic chromosomes—the pair *A*—is quite the largest of the spermatogonial complex. On the other hand, the smallest one—pair *L*—is among the smallest elements on the plate. The pair *A* often shows striking variations in form, one of the members often opening out so that the limbs form a much wider opened angle than

is usual (see fig. 5). The pairs *B* and *C* are J-shaped, but the shorter arm of *C* is at a smaller angle with the larger arm than is the case with the pair *B*. The pair *E* is also J-shaped and, while resembling *C*, is appreciably smaller. The pairs *F* and *L* are V-shaped and in each case the two arms are of approximately equal length. When the arms of the V's and J's lie in a plane perpendicular to that of the equatorial plate they simply appear as rods, and this is well demonstrated in fig. 2, where three of the J-shaped elements are not obvious.

Telomitic chromosomes. The rod-shaped chromosomes when aligned show a gradual decrease in size. The larger ones are placed with the flexed chromosomes at the periphery of the equatorial plate, while the smaller ones frequently move into the centre to lie with the microchromosomes. The largest pair is the fourth largest of the spermatogonial complex.

The pair *O* is considerably smaller than the pair *N* and yet definitely larger than the dot-like elements. At first I considered this pair as a larger pair of microchromosomes, since the two members often appear simply as rounded bodies slightly larger than the other dot-like elements. Later, however, they were clearly observed as small rod-like elements and consequently I consider that sometimes these small rods lie in a plane perpendicular to the equatorial plane and thus in polar view one sees only their ends. These bodies, therefore, obviously furnish a stage of transition between the smaller rods and the microchromosomes.

Microchromosomes. These appear as small, rounded, usually well-stained dots possessing no feature by which one is able to distinguish one from another. In well-preserved cells in which the other chromosomes are clear and well defined, their number is always six. At times, however, one or two of them were observed to be missing, and this was probably due to the fact that they were overlapped by the larger elements. As a rule they lie near the centre of the equatorial plate, but occasionally they show a tendency to wander out and place themselves more peripherally among the larger elements. I have never observed any lightly stained material joining the microchromosomes as described by Painter, and would agree with Matthey's observation on this point, that it is probably an indication of imperfect fixation.

The only previous account of the spermatogenesis of *Sphenodon* was published by Hogben (4) in 1921. This author made his observations on sections taken from the testis of a single individual fixed with aceto-bichromate. He refers to the frequency with which the heteromorphic elements are close packed and superimposed, and to the liability of confusing V-shaped elements with rods that are contiguous at one extremity. Further, the inconstancy in number and the aberrant behaviour of the dot-like elements led Hogben to deny the chromatinic nature of the latter and to consider them simply as stages in the disintegration of the plasmosome.

Now this close packing of the elements, the tendency to fusion of the individuals and the inconstancy in the appearance of the dot-like elements were precisely the factors which rendered my early studies on the material fixed with

Flemming and other fixing agents so difficult. Further, at this period I had not seen Hogben's paper, and it is therefore of great significance that my observations on this material led to the belief that the spermatogonial number was somewhere from 24 to 28, while Hogben tentatively advanced 26 as the probable number. But, as already indicated, the use of the Champy-Nakamura technique speedily produced a modification in this belief and revealed the inferiority of the fixation obtained by the fixing fluids containing acetic acid. In addition, the constant presence of the microchromosomes in many other reptiles, together with the equal constancy of their appearance and number in all the stages I have observed, can leave no doubt as to their nature. It is interesting to note that Hogben in his fig. 3 indicates the presence of 29 chromosomes, but figures seven small dots in addition, and again in his fig. 6 he shows 26 chromosomes with eight dots in addition.

(*b*) *Primary spermatocytes*

Diakinetic and metaphase stages of the first division were the most numerous in my material. Hogben was unable to arrive at any finality concerning the number of elements in the primary spermatocytes, but it is again of interest to observe in his fig. 16 the reproduction of 17 tetrads, four of which are dot-like elements and which for reasons stated above he excluded from his counts. I have always observed the presence of 18 tetrads—14 larger ones and four smaller rounded elements, one of the latter being, however, considerably larger than the other three. At metaphase the larger elements are grouped to surround the smaller. In the diakinesis (figs. 7 and 8) one can observe the tetrads opening apart to form single and double-ringed bodies and a median or sub-median attachment of the spindle fibre in the case of six of these is already indicated. In figs. 9 and 10, which represent a late diakinetic stage immediately before the tetrads assume their final position on the equatorial plate at metaphase, the morphology of the tetrads is shown more clearly than I have observed at any other period. Here on polar view there are six atelomitic tetrads appearing as double rings, one being considerably smaller than the other five, while the tetrads with terminal attachment appear as equatorial rings or rods. Here, then, there is an exact correspondence with the atelomitic spermatogonial chromosomes, of which there are five large pairs and one small pair.

Following the diakinesis, a more or less marked condensation of the tetrads appears to take place, so that on the equatorial plate at metaphase the appearances are very variable, as is obvious from an inspection of my figures. This condensation of the tetrads at the end of diakinesis has been described many times before and in many animals. Matthey (7), in discussing it, points out that the chief merit of the new technique lies in the fact that it has less tendency to cause this condensation of reptilian tetrads and thus permits a detailed study of their formation. He therefore considers that it is probably artificial, although he has not been able to eliminate it completely—"...je n'ai jamais obtenu de figures non condensées chez les Geckos et les Anolis." Concerning

this condition in *Sphenodon*, it is hardly possible to arrive at any decision without having, as pointed out above, more material for comparison. However, while some degree of condensation is always present, it varies in degree in different sections and often in different parts of the same section. It is therefore not improbable that to some extent, at least, it is artificial.

Fig. 12 represents a cell at metaphase in which practically all the tetrads were condensed and contracted and in which the largest tetrad appears as a double ring, while four of the other larger tetrads and one of the smaller ones appear as contracted dumbbell-shaped bodies. In contrast with this, fig. 14 represents a cell in which the contraction was much less marked, the largest tetrad appearing as a multiple-ringed body, four larger tetrads as double rings and one of the smaller ones as a dumbbell. These obviously correspond to the six double-ringed tetrads observed in the later diakinesis, the clear outlines of which have been somewhat obscured by the metaphase condensation. The smallest of the diakinetic double rings I have never observed showing the same patent appearance at metaphase. It always appears as a condensed dumbbell-shaped element, just as often happens in the case of the larger double rings. Thus the double-ringed tetrads when serially aligned (fig. 22) clearly correspond to the larger flexed spermatogonial chromosomes, while the dumbbell corresponds to the smallest V-shaped pair. In aligning the tetrads according to size an element of doubt is introduced owing to the condensation. If this is artificial, then it is possible that individual tetrads would be contracted in varying degrees. This would introduce errors into the determination of their relative magnitudes. However, I have drawn them up just as I have seen them on the equatorial plate, and it was certainly the case that the elements exhibited sufficiently clearly defined differences in size to render this comparatively easy. It was also the case that these differences corresponded exactly to those of the aligned spermatogonial chromosome pairs.

To return again to the structure of the tetrads, it is clear that in polar view six of them appear as double-ringed bodies. Fig. 11 represents one of them seen from the side and in slightly oblique view, and this tetrad is seen to be composed of three rings—one of which is perpendicular to the plane of the equatorial plate and the other two parallel to it. I have not had the opportunity of viewing all these tetrads in side view, but since they represent an essential similarity in polar view, there is no reason to suppose that they do not all conform to this type of structure. Thus, these six tetrads which appear in polar view as double rings are really composed of three rings, the middle one not appearing because it is placed in the plane perpendicular to the equatorial plate. In addition, it will be seen from the figures that one of these tetrads is considerably larger than the others and sometimes is seen to consist of three, four or five rings. It corresponds to the largest pair of spermatogonial chromosomes.

The formation of these ring tetrads is exactly similar to what Nakamura (9) has described in the case of *Natrix tigrina*, and thus corresponds to that of the ring tetrad common in the Orthoptera. The four chromatids are separated by

two splits—one on the equatorial plane and one on the reductional plane—so that three rings are formed, the middle one being perpendicular to the plane of the two lateral ones. Concerning the additional rings which appear in the largest of the tetrads, no particular observation has been made, and I can only suppose that the explanation of this appearance is similar to that advanced by Nakamura: "It is possibly due to the fact that one or both of the lateral rings of the original three rings remain twisted somewhat in the middle as a remnant of the strepsitene twisting, giving the ring the appearance of two rings instead of one."

The similarity of these ring tetrads to those of *Natrix tigrina* is very striking. They also appear in some of Matthey's figures and would appear to represent a fundamental type of tetrad formation in the Reptilia. It is of additional interest to note that this same type of tetrad formation is common in Amphibia.

The medium-sized tetrads corresponding to the rod-shaped spermatogonial chromosomes are very variable in their appearance on the equatorial plate.They sometimes appear as rod, wedge or Y-shaped bodies, and in other cases open out to form equatorial rings. I consider the latter to be their normal condition, as on comparing these elements carefully in different cells, I have found each of them at one time or another appearing as an equatorial ring. I further consider that the rod, wedge and Y-shaped appearances are due to condensation or to slightly oblique positions on the equatorial plate.

There are always four dot-like tetrads, of which one is considerably larger than the others, always presenting a condensed, rounded form. This obviously corresponds to the very short pair of spermatogonial rods, the other three corresponding to the six microchromosomes.

Anaphase material has been exceedingly scanty in my sections and I have not been able to make any observations on later anaphase. I was able, however, to observe the two good cells at commencing anaphase, which are reproduced in figs. 18 and 19. Here the tetrads were seen in side view commencing to draw apart, and while there was a considerable degree of condensation, six of them were clearly seen to have an atelomitic attachment of the spindle-fibre and one was obviously smaller than the others. For the sake of clarity I have omitted some of the tetrads from these figures. In fig. 18 two of the atelomitic tetrads appear as single axial rings and four as double rings—one ring being in the axial plane and the other parallel to the equatorial plane. In fig. 19 four appear as single axial rings and two as double rings. The appearance of this double ring in side view is very similar to that of the "Derby hat" tetrad, which Painter has observed to be so common in Mammals. It is formed, I believe, from the three-ringed tetrad seen at metaphase, by the opening apart of one of the side rings earlier on one side than on the other. Similarly, the single axial rings are produced from the three-ringed tetrads by the complete opening apart of both side rings. The smaller anaphase axial ring corresponds to the condensed metaphase dumbbell and this in turn corresponds to the small diakinetic element which appears in polar view as a double ring. Finally, a

consideration of the size differences of spermatogonial and primary spermatocyte elements shows that this small tetrad corresponds to the pair of small spermatogonial V-shaped chromosomes.

It is clear then that the primary spermatocyte of *Sphenodon* contains 18 tetrads. While the final confirmation of this is lacking, owing to the absence of anaphase stages, one is led to the conclusion from the above observations that six of them correspond in structure to the anaschistic V-shaped tetrad of Wilson (18), while all that one can say of the remainder is that the attachment of the spindle fibre is telomitic.

(*c*) *Secondary spermatocytes*

The lack of secondary spermatocytes in my material has been a very disappointing feature. Many observers have commented on the difficulty of studying these cells, their small size and the tendency of the elements to clump, rendering accurate observations exceedingly difficult. Painter (13) states that in mammalian spermatogenesis, the maturation divisions are probably the most sensitive of all stages to delay in fixation, and especially is this so in the case of the second division. Since Matthey and Nakamura have been able to study this stage with facility on suitable material, it would therefore seem that these difficulties, like many others, can be overcome by perfection of technique. In my sections a few secondary spermatocytes were occasionally observed, but the elements were so clumped as to render them of no value. I did succeed, however, in making one observation on the second division at anaphase, in which 18 monads were perfectly clear (fig. 20). Of these six are V-shaped with the arms rather widely opened, nine are rods—one being very small—and three are small dot-like elements. This is precisely what we should expect from the observations made on the spermatogonia and primary spermatocytes and adds support to the conclusions already arrived at concerning the presence of six anaschistic V-shaped tetrads in the first division.

(*d*) *Sex-chromosomes*

I have not observed in *Sphenodon* a chromosome nucleolus or karysome as described by Nakamura (9) in *Natrix tigrina*, nor have I observed anything in the behaviour of any of the chromosomes by which any pair of them could be identified as forming a sex-complex. However, the spermatogonial number has been found to be even and the 36 chromosomes can be grouped in pairs, the members of which are precisely similar in size and shape. Further, the formation and commencing division of 18 tetrads have been clearly observed and, finally, 18 monads have been recognised passing into the spermatid. It therefore seems highly probable that the type of sex-chromosome in this animal is *XX*. The male would then be homozygous in respect to sex, and this is just the condition which Matthey and Nakamura have found in many other reptiles.

IV. DISCUSSION[1]

From the above observations it is quite clear that the chromosomes of *Sphenodon*, as in several other reptilian families, can be divided into two sharply defined groups—larger elements or macrosomes and smaller dot-like bodies or microsomes. Matthey (7) considers this separation into two groups a primitive feature in the chromosome complex of Reptiles, though he was not able to observe it in *Sphenodon*. The section which Matthey examined was one which Dr Gowland took with him on his recent visit to Europe. Compared with the material I have used, it is so imperfectly fixed as to be devoid of any value. As to the presence of microsomes in *Sphenodon* there can be no doubt and this would support Matthey's view concerning their primitive nature. The very short pair of rods which form a transition between the spermatogonial macrosomes and microsomes I regard as belonging to the former class rather than to the latter. While they are smaller than the other rod-like elements they are at the same time appreciably larger than the microsomes and their rod-like nature is apparent. It is interesting to note that Matthey records the presence of a similar pair with dimensions intermediate between those of macrosomes and microsomes in a snake—*Coelopeltis lacertina*—and also the presence of two microsomes rather larger than the rest in an Autosaurian—*Ophisaurus ventralis*—a member of the family Anguidae.

I therefore consider that in *Sphenodon* there are $30M + 6m$. Of the macrosomes six pairs appear in the spermatogonia to have an atelomitic attachment of the spindle fibre. Further, as above mentioned, though the final proof of this has not been obtained by anaphase observations of the first division, it seems evident that the tetrads formed from them have also an atelomitic attachment of the spindle fibre. In other words the 12 **V** or **J**-shaped spermatogonial chromosomes form six anaschistic tetrads with median or sub-median attachment to the spindle. Therefore, the 36 chromosomes of *Sphenodon* can be grouped, in view of these observations, into three classes:

(1) Twelve atelomitic chromosomes which are **V** or **J**-shaped.

(2) Eighteen telomitic chromosomes which are rod-shaped.

(3) Six microsomes.

Robertson (16), in explaining the variations that occur in chromosome numbers in Orthoptera, advanced the opinion that **V**-shaped chromosomes are formed by the fusion at their proximal ends of two non-homologous rod-shaped chromosomes. He used the term **V**-chromosome in a general sense to include all two-armed chromosomes, whether **V**-shaped, **J**-shaped or **U**-shaped. This procedure I shall adopt here. Carothers (1) has pointed out that variations occur in the attachment of the spindle fibre, for he found in *Trimerotropis* and *Circotettix* that the point of attachment may change from a terminal to a non-

[1] For the sake of brevity of description and to avoid unnecessary repetition, the letter "*M*" is sometines used in place of the word "macrochromosome" and the letter "*m*" similarly represents "microchromosome." Further, "macrochromosome" and "microchromosome" are in places contracted to "macrosome" and "microsome."

terminal position even in the same chromosome pair. Thus, such a pair may sometimes appear as rod-shaped, at other times as V-shaped. In *Trimerotropis* the number of V-chromosomes varies from 7 to 17, but the type number of 23 is always found in the spermatogonia. Consequently, it cannot be maintained that V-chromosomes invariably arise from the linkage of two rods. Nevertheless, as a general working principle this view of the origin of the V-chromosomes has been of great value. The manner in which it has permitted the variations in chromosome number, both in the Orthoptera and Diptera to be reconciled has been remarkable.

Matthey (7) has applied this idea in an attempt to explain the evolution of the chromosome formula of the Autosauri, with results of the greatest interest. Since the principal importance of the present study lies in the relation of the facts it presents to the findings of Matthey, it is necessary to summarise here the salient features of those findings.

Matthey (7) points out that the Reptilia have arisen from the Amphibia and have in turn given birth to the Mammalia. Now the fundamental or type number of chromosomes in the Amphibia is 24. Of the Mammalia while the Eutheria appear to have a type number of 48, the more primitive Marsupials would seem to possess a type number of 24. Matthey, therefore, supposes that the fundamental reptilian number is 24 and further, that these are 24 telomitic elements. Then, considering a V-chromosome as representing two rod-shaped elements, it is found that in six families of the Autosauri, viz. Anguidae, Xantusiidae, Varanidae, Helodermatidae, Agamidae and Iguanidae, the number of macrosomes present is in each case equivalent to 24 rod-shaped chromosomes, the ratio of V-chromosomes to rods varying in different cases. In addition, all these families further agree in possessing 24 microsomes. These six families thus make up "le complex iguanoïde" in which a basic chromosome complex of 24 telomitic $M + 24m$ is common to each member, and this is the primitive reptilian condition. Other families which show a modification of the latter are derived from this primitive group. Thus *Chamaeleon vulgaris* has only 12 microsomes, but these are larger than the microsomes found in the families named above and have arisen from a pairing two by two of the primitive 24 elements—while *Aniella pulchra* which has eight small elements—larger, however, than those in *Chamaeleon vulgaris*—has obtained these by a fusion of the 24 microsomes three by three.

In the case of the Anguidae the factor of translocation is introduced. Thus in *Pseudopus apus* there are 20 macrosomes + 24 microsomes. Of the former, there are sometimes $4V$ and sometimes $2V$, and this in the same animal. In the type with $4V + 16$ rods we are again brought to the basic number of 24 telomitic rods. The type $2V + 18$ rods is produced from this secondarily by a translocation of the spindle fibre attachment in the case of two of the V-chromosomes, i.e. two pairs of rods fuse at one end, but by an inversion of the segments the spindle attachment becomes telomitic instead of being at the apex of the compound element. Hence, the latter appears in the gonia as a rod

instead of a *V*. Translocation therefore produces a secondary condition in which the fundamental number of 24 telomitic elements appears as 22. This process is also advanced as a possible explanation of the state found in *Gerrhonotus kingi*, which has 21 elements, including one *V*; in *Anguis fragilis* having 19 elements, of which there are 2*V* and in addition a compound rod; and in the Zonuridae in which there are 22 telomitic elements. In the latter, though all the gonial chromosomes have a terminal attachment, one pair constantly appears sharply flexed—a significant observation from which it is inferred that the members of this pair, formerly V-shaped with median attachment, have now become telomitic owing to translocation of the attachment of the spindle fibre.

A second group—"le complex scinco-lacertoïde"—is characterised by the presence of 36 elements presenting when aligned a gradual decrease in size. This complex is held to be produced by a reduction in size of the macrosomes and a fusion two by two of the microsomes, and this is inferred from the observation that in *Scincus officinalis* there is a sharp differentiation between 24 elongated elements and 12 more rounded elements. The former represent the reduced 24 macrosomes of "le complex iguanoïde," and the latter the 24 macrosomes of this complex fused two by two.

The Anguidae, then, which superficially appear to present a condition aberrant from the basic one, can on analysis be reconciled with the fundamental scheme. The latter is clearly obvious in six families and appears slightly modified in the Zonuridae, Aniellidae and Chamaeleontidae—in the first case by translocation and in the latter two families by fusion of the microsomes. From "le complex iguanoïde," "le complex scinco-lacertoïde" is directly derived by reduction in size of the larger and fusion of the smaller elements, and this comprises the families Scincidae, Lacertidae and Tejidae.

The only family of the Autosauri, so far investigated, whose chromosome complex does not fall into this fundamental scheme is the Geckones, which appear to possess 42 telomitic elements. In view of what has been observed in *Sphenodon*, this is very significant. The Autosauri, then, can be grouped into two main classes according to chromosome condition. The majority of the families fall into a group in which a fundamental complex of 24 macrosomes + 24 microsomes is common to all the members. In the second group are the Geckones possessing 42 rod-shaped elements.

Now, applying the theory of Robertson to the case of *Sphenodon*, we suppose that the 12 *V*-chromosomes are compound elements and correspond to 24 rods joined two by two at their proximal extremities. It is true that one pair of *V* elements is smaller than the corresponding elements observed in other Reptiles, but at the same time I see no reason why it may not also be considered as a compound chromosome. These 24 rods derived from the flexed chromosomes, together with the other 18 rods present, make a total of 42. Thus the chromosome complex of *Sphenodon* is equivalent to $42M + 6m$, giving a total of 48 elements. As we have seen, Matthey considers that the majority of Autosauri

also have as a fundamental number a total of 48 elements, while the Geckones present a total of 42 rod-shaped chromosomes. It is therefore a striking fact to find *Sphenodon* possessing also a total of 48 elements, of which 42 are rods, and there is ample justification for considering this total number of 48 elements as the primitive chromosome complex of the Reptilia.

This primitive number, though considerably modified in different cases, has been retained by modern Reptiles, the Geckones retaining unaltered the same 42 telomitic elements that we have seen in *Sphenodon*, while the majority of Autosauri retain 48 elements. With the first statement we may correlate the interesting fact that the Geckones are held by modern zoologists to be an ancient and early isolated branch of the Autosauri. To quote Gadow (vol. III, p. 500), "Geckones are probably the oldest of modern Autosauri" and (p. 503) "The Geckos seem to be not only a very independent but also a very old branch of Saurians." This view would surely gain additional support from the striking similarity of the number of rod-shaped chromosomes in this family to that possessed by the extremely primitive and generalised *Sphenodon*.

Of the fundamental 48 elements found in the majority of the Autosauri, 24 are microsomes. Matthey was unable to advance any explanation of the presence of these elements, but considered them to be a primitive feature of the reptilian complex, and further, the presence of 24 of them to be also primitive. They are certainly present in *Sphenodon*, but their number is much reduced—there are only six. Also in this animal the two very small rods provide a very clear transition between the rod-like macrosomes and the dot-like microsomes. Now Wilson (18) states as one of the possible means by which permanent changes in chromosome number have been produced "a gradual reduction in size and final disappearance of individual chromosomes, a process that may be connected with a corresponding dropping out of genetic factors or a redistribution involving a transfer of their substance to other chromosomes." I would suggest it as possible that this process has played a part in the evolution of the chromosomes of Reptiles. Accordingly, I would postulate firstly that the basic and primitive number in Reptiles is 48 rods. In *Sphenodon* there has been a slight change involving a decrease in size of six of these elements, possibly, as Wilson says, by a dropping out of genetic factors or a transfer of their substance to other chromosomes. In the Geckones this process has gone slightly further and these six elements have been completely lost, while the early separation of this family from the main line of descent of the Autosauri has permitted it to retain its primitive heritage of 42 rods little changed.

Matthey supposes that this main line of descent of the Autosauri commenced from a form richly endowed with potentialities for change and that this form possessed 24 macrosomes + 24 microsomes. I would consider it possible that this combination was derived from the primitive reptilian number by a more extensive process of reduction involving 24 of the 48 primitive rod-like elements. From this form the modern families could still have been derived in the manner which Matthey has suggested. Further support to my view would seem

to be given by the Chelonians, which zoologists agree have evolved, probably from the Prosauria, along a line of descent distinct from that taken by Autosauri. An insufficient number of forms have yet been examined to permit of any definite statement concerning the primitive Chelonian condition. However, Matthey observes in *Emys europaea* the presence of 50 chromosomes, including four *V*-chromosomes. These would correspond to 54 telomitic rods. In *Testudo graeca* the number appears to be between 54 and 60. It is likely, therefore, that the fundamental number in the Chelonian group is between 50 and 60, and it would seem that this group has tended to retain the primitive complex of 48 rods to a greater extent than the Autosauri and has modified it in a different manner, probably by a fragmentation of some of the chromosomes. This would explain the fact that the type number of the Chelonians promises to be in excess of 48.

Of course, it is realised that any attempt to formulate a scheme designed to show how changes have occurred in chromosome groups passing from species to species or family to family must remain for the present of a purely provisional nature. It has been argued that evolution of chromosome numbers has followed a course too fitful and irregular to justify any such attempt being made. But, on the other hand, many interesting facts have been gleaned from the study of these changes in the vegetable kingdom, and on the evidence we have at present there seems to be little doubt that polyploidy and duplication of chromosomes have played some part in the formation of new plant species. To this problem in the animal kingdom much less attention has been paid, due no doubt in the case of the higher Vertebrates to a lack of knowledge of the form and number of the chromosomes in a sufficient number of species. Painter (14), however, has presented a most convincing statement concerning the relations which exist between the chromosome numbers in the different groups of Mammals, and the facts which have emerged from a similar study of these in Reptiles, even though the investigation of the latter is as yet incomplete, certainly warrant the hope that this field of study will not lack interest and value.

It only remains for me to point out the relationship which the primitive reptilian chromosome number bears to the mammalian. The study of the facts observed in *Sphenodon* has led me to suggest that the primitive number of chromosomes in Reptiles is 48 telomitic elements. Painter (14) has arrived at the conclusion that in the *Eutheria* the primitive number is also 48 and that though the type number in the Marsupials appears to be 24, the total amount of chromatin seems to be about the same in the two groups. As he points out, "in one case it appears in large packets, so to speak, while in the other we have smaller aggregations." These relationships would seem to be decidedly significant.

V. SUMMARY

1. The number of chromosomes in the spermatogonia of *Sphenodon* is 36, i.e. 12 V or J-shaped, 16 rods, two very short rods and two microchromosomes.

2. The equatorial metaphase plate of the first division shows 18 tetrads, six of which have an atelomitic attachment of the spindle fibre, and the remainder a telomitic attachment.

3. The atelomitic tetrads are similar in structure to the anaschistic V-shaped tetrads of other Reptilia and also to the ring tetrads of the Orthoptera. The telomitic tetrads usually appear as equatorial rings.

4. Secondary spermatocytes were rare, but one observation on the second division at anaphase showed clearly the presence of 18 elements, i.e. six V-shaped, nine rod-shaped and three dot-like.

5. From the observations made, it is highly probable that the male is homozygous in respect to sex, the condition of the sex-chromosomes being *XX*.

6. Applying the theory of Robertson concerning the formation of V-shaped chromosomes to those of *Sphenodon*, it is possible that the primitive number of chromosomes in the reptilian order is 48. It is suggested that the chromosomal formula of the Autosauri has been derived from this primitive number principally by a reduction in size of the individual elements.

I wish to express my thanks to Dr W. P. Gowland, firstly, for making it possible for this work to be done, and secondly, for his unstinted enthusiasm, encouragement and advice which have greatly accelerated its progress.

I also desire to acknowledge a debt of gratitude to Dr A. Durward, formerly Senior Demonstrator in this Department, for the stimulation of his encouragement and assistance at the commencement of these studies.

Lastly, I wish to thank Dr R. Matthey, of the University of Lausanne, for his great kindness in putting at the disposal of this Department the details of the Champy-Nakamura technique.

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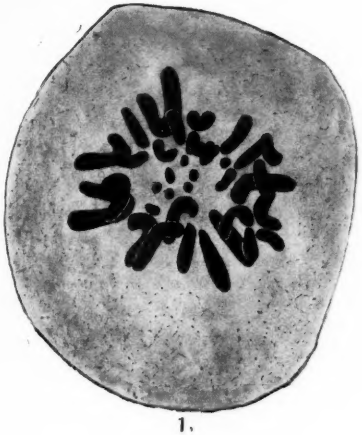
A full review of the literature relating to this subject is given by R. Matthey in Number 7 of the above list.



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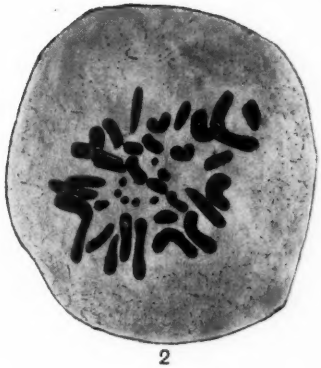

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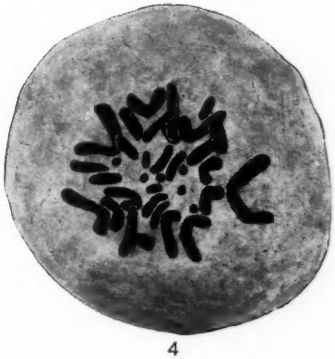

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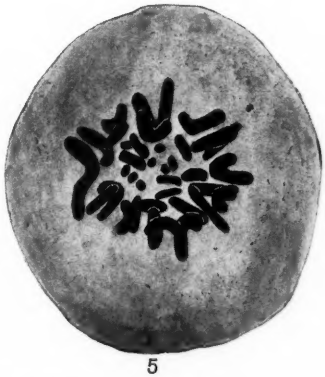

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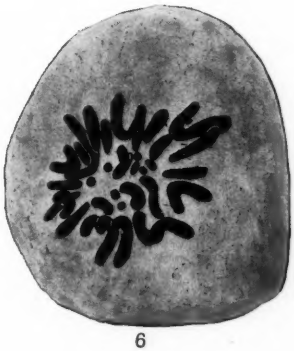

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KEENAN—The Chromosomes of Sphenodon punctatum

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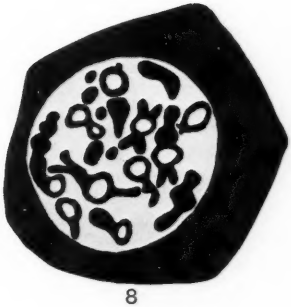

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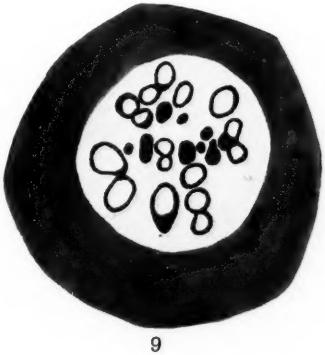

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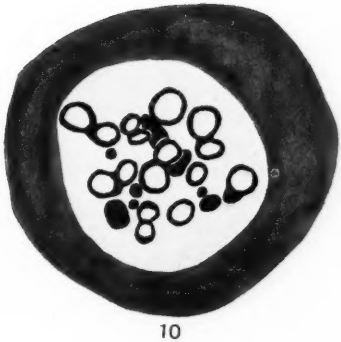

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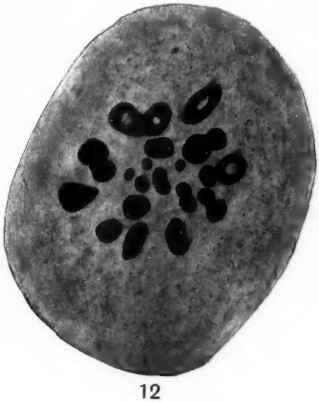

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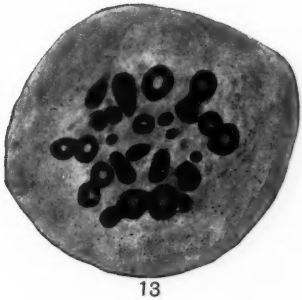

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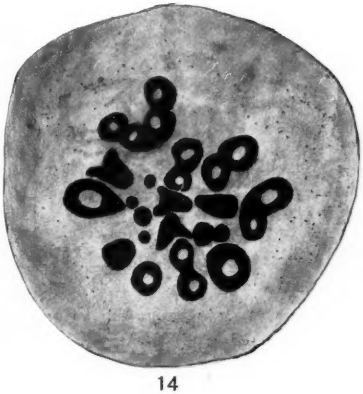

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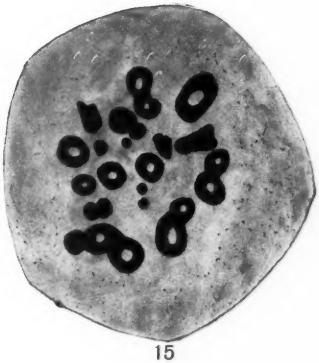

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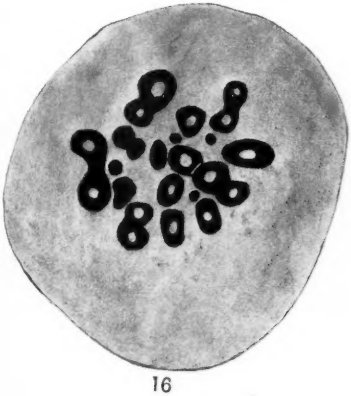

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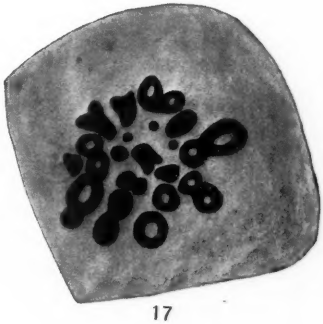

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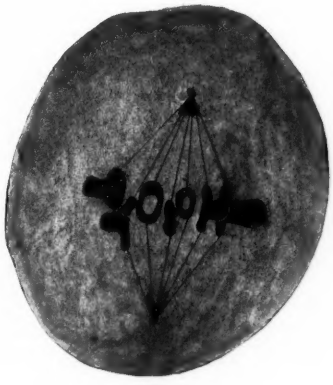

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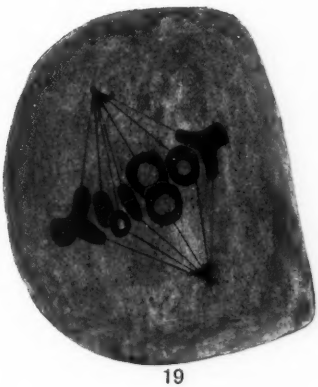

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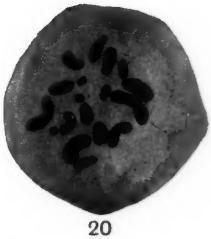

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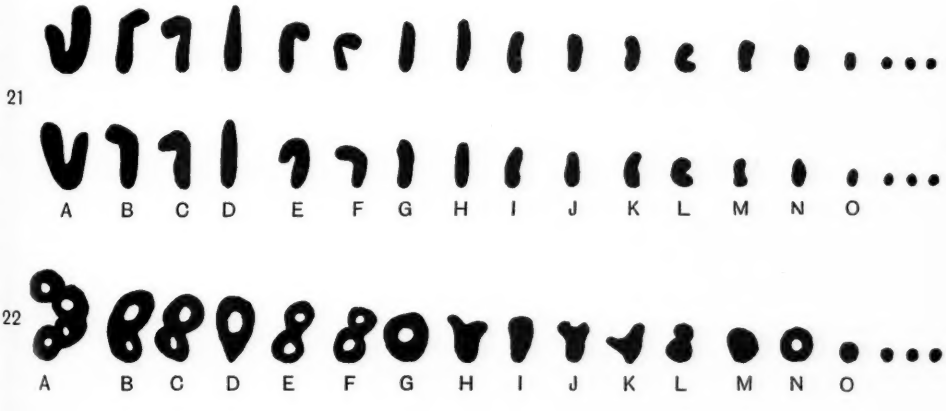

EXPLANATION OF PLATES

All the figures were drawn at a magnification of 2700 diameters and have been reduced by one-third. A camera-lucida was used, together with a 1/12th oil-immersion (Leitz) and a No. 20K ocular (Zeiss).

PLATE I.

Figs. 1–6. Equatorial plates of the spermatogonia in polar view. Thirty-six chromosomes are seen in each figure.

PLATE II.

Figs. 7–8. Primary spermatocytes in the diakinesis.

Figs. 9–10. Primary spermatocytes in the late diakinesis.

Fig. 11. One of the late diakinetic tetrads seen from the side and obliquely.

PLATE III.

Figs. 12–17. Polar views of the equatorial plates of the primary spermatocytes. Eighteen tetrads are seen in each figure.

PLATE IV.

Figs. 18–19. Primary spermatocytes at the commencement of anaphase.

Fig. 20. Polar view of the equatorial plate of a secondary spermatocyte.

Fig. 21. The synaptic mates of the spermatogonial chromosomes drawn up in serial alignment (from fig. 1).

Fig. 22. The tetrads of the primary spermatocytes at metaphase drawn up in serial alignment (from fig. 14).

THE DISTRIBUTION OF SYMPATHETIC FIBRES IN THE EXTREMITIES

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Though there can be little doubt that sympathetic nerve fibres are distributed to the vessels and other structures in the extremities along with the cerebrospinal nerves and are arranged like these on a segmental plan, yet other views have been put forward. It has been suggested that they proceed to the periphery along the coats of the blood vessels, and this has led to the operation of arterial sympathectomy for certain diseases. Again the view has been expressed that, although the blood vessels are fed with vasomotor nerves, yet these vasomotor nerves are more numerous in certain parts than in others. Evidence has been put forward by Todd and his co-workers that the vasomotor supply in the region of the digits and distal part of the limb far exceeds that which occurs in the more proximal part of the extremity.

The mode of distribution of the sympathetic is obviously of considerable practical importance. In those conditions of supposed angiospastic origin the hands (or feet) and digits are affected in such a way that the vascular lesions correspond to no known nervous distribution. This naturally is a substantial argument against the theory of a nervous origin of such a pathological state.

The irregularity of the way in which the digits are affected may be seen from the list which has been abstracted from a well-known monograph. The author cites a series of cases of Raynaud's disease, and in some the disease began in the third, fourth and fifth fingers, and later the index finger and thumb were involved. Again in other cases all the fingers were involved with the exception of the minimus. It is obvious that no such distribution, as indicated by the above dispersion of the vascular lesions, can be fitted into any scheme of nerve distribution and certainly does not support any claim of a primary nervous origin of Raynaud's disease.

On the other hand, the topographical distribution of the grey rami in the cervical roots has been invoked to explain the many vascular disturbances that are deemed to be associated with the pressure occasioned by the presence of a cervical rib. Thus recently Telford and Stopford (1930) encountered a case of cervical rib in which the vascular changes began earliest and proceeded furthest in the index finger. By histological investigation Stopford discovered that there was a bundle of non-medullated fibres in the first dorsal root so situated that it might be expected to suffer immediately from the pressure of the cervical rib. This anatomical arrangement seemed to the authors to furnish them with a

convincing explanation of the vascular and trophic changes that ensued in their case.

If, however, the sympathetic fibres are distributed along with and in the same manner as the other components of the brachial plexus, then it would be surprising to find that pressure on the first dorsal and its grey ramus should involve the index finger. Admittedly there is great divergence in the territories allocated to the various segments of the brachial plexus, yet no one has brought the index finger within the segmental area of the first dorsal.

The investigations of Langley can hardly leave any doubt that vasomotor fibres, like the sudomotor and the pilomotors (whose segmental distribution he investigated and proved in a great variety of animals), are distributed in a segmental manner. Nevertheless many anatomists have not accepted that this is proven for the sympathetic fibres of the limbs. Waterston, in his recent book on Surface Anatomy, observes that the segmental distribution of the peripheral sympathetic is still doubtful. Perhaps the obvious breaks in the segmental arrangement of the pre-ganglionic fibres occasion the suspicion that the peripheral system may also be anomalous.

METHOD OF INVESTIGATION

For these various reasons it seemed desirable to us to furnish proof, if we could, of the distribution of the sympathetic nerve fibres in the extremities of Man. The method we decided upon was to inject the nerves of one of us with novocaine and in that way temporarily paralyse the vasomotor fibres running in the injected nerve. The flush that would follow the release of the blood vessels from their constrictor tone could be observed and the rise of temperature measured by means of a thermopile. We soon discovered in the course of our preliminary experiments that certain precautions are necessary. The room in which the experiments are performed should be at a constant and comfortable temperature. The two extremities may differ considerably from each other in temperature and particularly the different digits of the same hand may diverge considerably from one another. For instance, the ulnar side of the hand and the little finger are usually colder than the radial side. In order to get rid of these differences it was found desirable to bring the hands and forearm to the same temperature by plunging them into water at about 25° C., and keeping them there for about 15 min. It was then found that symmetrical spots on the two hands would keep the same temperature for a long time if the room itself were at a constant and comfortable temperature. Without these precautions it was of interest to note that symmetrical spots on the two hands were more likely to be of the same temperature than two spots on the same hand. For the thermopile and mirror galvanometer scale we used we are indebted to Prof. Hopwood, of the Department of Physics, St Bartholomew's Medical College.

The larger nerves, like the ulnar and the median, were found by the ordinary landmarks. The smaller cutaneous nerves, like the lateral and medial cutaneous, were discovered by exploring with a faradic electrode and recognised by the

spread of a characteristic sensation throughout their area of distribution. This enabled one to inject them most accurately.

The effects of injection

After some trial and error we used 2–4 c.c. of 4 per cent. novocaine with 1 in 60,000 adrenalin. This amount produced complete anaesthesia and vasomotor paralysis, but either produced no or only the very slightest motor paralysis.

In the beginning of our experiments we omitted the adrenalin, since we presumed that in experiments designed to bring out a vasomotor paralysis the use of adrenalin might be a complicating factor. We soon discovered, however, that without adrenalin the novocaine was rather ineffective. The addition of adrenalin enhanced its power of nerve blocking very considerably. It was obvious that the effect of the adrenalin was quite local and confined to the region of the injection and so did not complicate the experiments as we feared.

This experience led us to consider why the adrenalin enhanced the effect of the novocaine so much, even when this was injected directly into the nerve trunk. The most likely explanation was that it prevented the escape of the novocaine into the blood vessels of the nerves. This led us to investigate the manner in which nerves receive their blood supply.

Blood supply of nerves

We were able to investigate this anatomical problem readily, for we had made some injections of barium emulsion into amputated limbs. We examined the larger nerve bundles with a binocular microscope, by means of radiograms, and studied them after they had been cleared by the Spalteholtz method.

From our observations it is clear that nerves are much more vascular structures than one might infer from the nature of the physiology of nerve processes or from the appearances they present when examined by the ordinary method of dissection. A large nerve trunk possesses an axial artery of considerable size, and this is continued along the long axis of the nerve being fed by fair-sized arterioles at intervals of about every 3 to 5 cm. This axial blood vessel divides when the nerve trunk divides and so is continued into its branches. In the larger trunks this axial stem is embedded in the substance of the nerve, but in the smaller branches it lies immediately adjacent to the nerve and wrapped in the same connective tissue sheath. The nerves to the muscles and the cutaneous nerves are accompanied in the same way by a parallel blood vessel, and this in the case of, say, the nerve to the extensor proprius hallucis, may run very far without receiving any tributary vessel. We suppose therefore it is by the obliteration or constriction of these vessels that adrenalin so enhances the effect of novocaine when injected into nerve trunks.

Order of disappearance of the nerve functions

We found that the flush and warmth due to the vasomotor paralysis came on early and was quickly followed or was simultaneous with the loss of sen-

sation to prick. Heat and cold we did not particularly test for. Touch was lost later than prick, but in all cases the loss to both prick and touch seemed to be of the same extent. We found no evidence of dissociation. It has already been remarked that our methods and dosage led to no real loss of motor power. We also observed that even with complete digital anaesthesia there was no loss of the sense of the awareness of the position of the finger and we could place the fingers in any desired position. This surprised us in view of the evidence brought forward by Stopford that the nerves of deep sensibility to the fingers run by way of the digital branches.

In anaesthetising the various nerves we were struck by the observation that a loss of sensation which did not involve the hand and digits occasioned no inconvenience, was quickly forgotten, and one would be almost unaware of it unless looked for. Quite different was the case when the hand and the digits were involved, for then the oddness of the state kept on intruding itself in consciousness. The awareness of the unusual state persisted as long as the anaesthesia endured and one could not let the hand alone. The desire to rub it and interfere with it was irresistible.

The order in which the different functions of the injected nerve disappeared invites consideration. Ranson (1931) has recorded somewhat similar observations and boldly declares that this order of disappearance coincides with the difference in size of the nerve fibres. Those which are smallest, as might be expected from a process which depends on diffusion, are the first to be interrupted, while the largest are affected last. Ranson indeed regards this dissociation effect of cocaine as being a corroboration of his hypothesis that pain fibres are either non-medullated or very finely medullated. We have already remarked that motor effects were extremely slight in our experiments, and more confidence might have been felt in the hypothesis that the nerves affected by the diffusion of the novocaine are first the smaller and then the larger fibres, if there had been some motor effect. Though perhaps the motor fibres as a whole are coarsely medullated, yet it has been shown by Sherrington (1931) recently in his work on the fractionation of muscle contraction that there are motor fibres even of the order of 2μ.

Vasomotor effects of nerve injection

About twenty experiments were performed in which different nerves and several injections of the same nerves were made. We shall set forth now what we observed in several of these cases.

Three c.c. of novocaine were injected into the ulnar nerve of the left upper limb as the nerve passed behind the medial condyle. Readings with the thermopile were taken from the index, ring and little fingers, from the radial and ulnar sides of the palm, from the radial and ulnar sides of the forearm. Twenty minutes after the injection anaesthesia was apparent in the area usually allotted to the ulna, i.e. the ulna half of the ring finger, the little finger, the ulnar margin of the palm including the hypothenar region on the volar aspect and the dorsum as far as the metacarpal of the ring finger. The dorsal aspect of

the first and second phalanx of the ring finger escaped the anaesthesia. The anaesthesia extended to the forearm along the ulnar margin for a distance of about 2 in. Over the same area there was a distinguishable flush and a rise of temperature easily perceived in the little finger. This rise of temperature, measured by the thermopile, reached in the case of the little finger 2° C., along the ulnar border of the palm to about 1° C., and along the ulnar border of the forearm it was difficult to distinguish that there was an actual rise of temperature. On the dorsum the changes in temperature were less marked and amounted to 1·3° C. on the little finger, while on the dorsum of the hand and forearm no changes in temperature were detected.

It was clear then that in the case of the ulnar the vasomotor nerves were running with the branches of distribution of the ulnar, for the effects of vasomotor paralysis coincided with the distribution of that nerve and the alteration in temperature confirmed this. It is to be noted that the change of temperature is greatest distally and less marked proximally.

Blocking the median nerve at the wrist gave rise to an anaesthesia in the region of that nerve which coincided with the customary distribution of that nerve. In the region of the three-and-a-half outer digits there was a rise of 2° of temperature. A difference between the two sides of the ring finger was perceptible, and the thermopile showed that the radial side was 0·5° hotter than the ulnar side.

In contrast with the previous experiment the median nerve was blocked in the antecubital fossa with 2·5 c.c. of novocaine with adrenalin, and the temperatures were taken over the several fingers, over the palm and forearm, and the dorsal aspect of hand and forearm as well. Both hands and forearms had been brought to the same temperature by immersion, and preliminary readings showed that the temperature was the same on the two sides at the same places. The anaesthesia followed the usual distribution of the median. The readings on the scale were as follows:

(Three cm. on the scale equal 1° C. The lower readings indicate a rise of temperature.)

	Left (anaesthetic side)	Right (control side)	Rise of temp. ° C.
Little finger	31·8	32·2	0·13
Ring finger	15·8	30	4·8
Middle finger	14·7	27	4
Index finger	13·2	21·6	2·8
Thumb	11·5	18·8	2·4
Wrist	13·1	20	2·3
Middle of forearm	19·5	19·8	—
Antecubital fossa	17·1	17·8	—

The temperatures were also taken on the dorsal aspects of the fingers just proximal to the nail bed in each case. These showed approximately an increase of 1° C. in the case of those digits within the distribution of the median.

Attempts were made to inject such nerves as the musculo-spiral and the dorsal interosseous. Though we succeeded in producing anaesthesia over the region of the cutaneous fibres of the musculo-spiral, we were unable to find any evidence of vasomotor effects beyond those attributable to the anaesthetisation

of such branches as the dorsal cutaneous branch of the forearm. By means of a faradic stimulus we defined the position of such nerves as the medial and lateral cutaneous, and injected these. Anaesthesia corresponding to their distribution was obtained and within this area the skin became smooth and slightly flushed. In fact it was easy to determine the cutaneous area belonging to the nerve by the feel of the skin. When we came to measure the change of temperature within the area of these nerves, i.e. the medial, the lateral, and the dorsal cutaneous, though it was clear the pilomotor and vasomotor nerves had been affected, it was not possible to show that there was anything more than the slightest rise of temperature.

We made peri-arterial injections about the radial and ulnar arteries, and in no case were we able to see any changes that would follow if the vasomotor nerves had been put out of action and no change in temperature could be elicited by means of the thermopile.

We injected the musculo-cutaneous nerve in the leg and also the posterior tibial close to where it gives off the medial and lateral plantars. In the former case only slight changes were elicited, but in the case of the plantar nerves the changes were obvious. The area of anaesthesia embraced the whole plantar surface of the foot and extended on to the dorsum of the toes. The flush corresponded with the area of anaesthesia. There were no motor effects. The injection consisted of 3 c.c. of 4 per cent. novocaine and 1 in 60,000 adrenalin. The anaesthesia extended on to the medial aspect of the ankle around the site of injection. It was fully developed in 20 min. The heat of the foot was easily perceptible and the veins leading from the foot were swollen and obvious.

Readings before anaesthesia developed

(In centimetres from the scale. The lower readings mean a rise of temperature. 3 cm. equal 1° C. Injection made at 4.45 p.m.)

Readings at 4.47 *p.m.*

	Right side (control)	Left side (plantar nerves injected)
Great toe	41·6	43·6
2nd toe	45·0	47·1
3rd toe	45·8	45·8
4th toe	39·8	38·0
5th toe	38·4	39·5
Front of sole	39·2	37·7
Middle of sole	33·6	33·3
Back of sole	33·5	31·5

Readings at 5.10 *p.m.* (30 min. after injection)

	Right side (control)	Left side (injected)
1st toe	41·9	19·5
2nd toe	41·7	17·3
3rd toe	40·7	17·3
4th toe	40·1	17·1
5th toe	39·2	16·1
Front of sole	37·0	16·2
Middle of sole	34·0	17·9
Back of sole	35·4	16·6

In the case of the musculo-cutaneous, the rise of temperature was not more than $\frac{1}{3}°$. In the case of the plantar, a rise of temperature has occurred of approximately about 6°.

These experiments were repeated many times with always the same result. Vasodilatation from paralysis of the vasoconstrictors occurred when the nerves were injected with novocaine, and the evidence of this vasoconstrictor abolition, viz. the flush, the subjective sensation of warmth, the heat perceptible to the feel, and as measured by the thermopile, were coterminous with the cutaneous innervation of the nerves injected. The two sides of the ring finger gave an excellent test case for the ulnar and the median, and the differences enumerated above could be distinguished on the radial and ulnar sides according to which nerve was injected.

DISCUSSION

It is consistent with most previous work on the sympathetic that its peripheral distribution in the limbs should run with the peripheral nerves and have the same distribution. The results obtained by injection confirm in every way this idea of the distribution of the sympathetic and afford no evidence that they follow the way of the blood vessels.

Though we do not feel enough confidence in our thermopile to discuss the smaller differences in temperature that we encountered, yet we feel that the larger results are sufficiently valid to be considered. It is clear that the greatest change of temperature occurs in the region of the digits and is much greater on the volar aspect than on the dorsal. The difference is considerable on the palm and sole, but grows less as one advances more proximally. Such nerves as do not supply the palm or the digits give only a small change of temperature within their area, though it is quite clear that there is a vasomotor change and also a paralysis of pilomotor nerves. The changes dependent on paralysis of sympathetic fibres can only be elicited where the nerves become cutaneous. Motor nerves, for instance, like the dorsal interosseous or the motor nerves of the median in the forearm, by our methods gave no evidence of the presence of vasoconstrictor nerves being paralysed by the injection. It is known that sympathetic fibres do run in the motor nerves, and it is also generally agreed that they are not very numerous. Apparently they are not numerous enough to produce an effect detectable by the apparatus we used. This predominance of vasomotor effects in the distal parts of the limbs may depend on the innervation or on the kind of blood vessels present. Grant and Bland (1931) have brought forward evidence emphasising the importance of the anatomy of the blood vessels in these parts.

If we accept these results, namely that the blood vessels of any area are under the regulation of the vasomotor nerves that run with the segmental nerves of that particular area, then it is difficult to refrain from considering how this arrangement has come about. The fully developed vessels of an extremity with their great axial stems do not easily fit into such a segmental

scheme. If we go back to the beginnings of the vascular pattern of the limb perhaps the matter is less obscure. In a previous paper one of the authors investigated the manner in which the vessels develop. It was apparent that the old crude idea of the vessels growing into the limb, as though they bored their way from the attachment of the growing limb to the trunk out towards the periphery, was quite inadequate. As a matter of fact as soon as vessels can be detected at all it is apparent that the whole of the growing limb bud is filled with a capillary plexus which is connected to the trunk by a series of segmental vessels, corresponding to about the number of segments that go to make up the limb. It is true that all but one of these vessels—in the upper extremity, the seventh segmental—soon disappear, and this one alone continues to enlarge and becomes the axial adult vessel. Out of the capillary bed other definitive vessels are developed according to the needs of the growing member, and these in their turn become the named arteries of ordinary descriptive anatomy. We assume, therefore, that the earliest capillary bed connected with a series of segmental vessels is the basis on which the segmental innervation of the vessels is achieved. On this presumption a large arterial stem would be innervated according to the segmental value of the capillary bed out of which it arose. It is not possible at the moment to prove this, for although it is known that a large artery like the brachial, or radial, or ulnar for instance, receives many branches from the adjacent nerves, it has not been possible, so far as we know, to determine what segmental nerve or nerves are thus reaching the vessel.

SUMMARY

1. The vasoconstrictor nerves and other sympathetic fibres pass to the periphery with the ordinary cerebro-spinal nerves.

2. They have precisely the same distribution as these nerves, i.e. the sympathetic fibres in the median or ulnar or other nerve are limited to the same territory as these nerves innervate.

3. The line of demarcation between the sympathetic nerve fibres of peripheral nerves is as sharply defined as are the limits of cutaneous innervation. The ring finger, for instance, receives sympathetic fibres from the median on the radial side and from the ulnar along its ulnar border.

4. The effects of cutting off the vasoconstrictor innervation are most marked in the digits and palm, and become less marked as one advances proximally along the limb.

5. The methods used in these experiments have not revealed the sympathetic fibres going to vessels of the muscles. It is inferred therefore that these must be few in number.

6. The same methods excluded the transmission to the periphery of vasomotor fibres in the adventitia of larger blood vessels.

ABSTRACT OF SOME OF THE EXPERIMENTS

Exp. 4. *Median nerve at wrist*

After 5 min. the thumb showed a rise of 1° over the little finger; and after 25 min. a rise of 2°. The nail bed of the thumb showed a similar increase of temperature.

In this experiment the hand was placed in a box; but it was found that the increased temperature of the anaesthetic area led to a rise in temperature, though of less degree, in the nonanaesthetic area also. Hence differences in temperature are more easily observed and of greater degree if the hand is not confined in a box; constant external conditions must, of course, be maintained.

Exp. 5. *Radial nerve (forearm in a box)*

The anaesthetic area showed a slight flush, but no detectable rise of temperature.

Exp. 6.

This showed that corresponding points of opposite limbs were at the same temperature, and greatly simplified subsequent work. Previously, the variations in temperature between two closely adjacent areas made assessment of the findings difficult.

Exp. 7. *Musculo-spiral nerve in arm*

Neither anaesthesia nor flush resulted.

Exp. 10. *Ulnar nerve at elbow*

Only slight anaesthesia developed, and the rise of temperature averaged only $\frac{1}{3}$°. Thus demonstrating that the degree of vasomotor paralysis varies *pari passu* with the depth of anaesthesia.

Exp. 11. *Medial cutaneous nerve of forearm*

No temperature differences obtained. Neither hot nor cold immersions showed any differences in temperature, or in rate of warming or cooling between the two sides. (Exp. 16 showed this also.)

Exp. 12. *Left median nerve at elbow*

The scale readings show the rise in temperature in the left index finger.

	Right (control)			Left (injected)		
	Index		Little	Index		Little
Distal phalanx	21·6		32·2	13·2		31·8
Volar metacarpal	17·2		22·6	10·0		20·2
Nail bed	15·0		—	11·5		—
Dorsal metacarpal	17·2		—	12·9		—
Wrist		23·8			17·9	
Forearm		19·7			19·5	
Antecubital fossa		17·8			17·1	

Exp. 15. *Left ulnar nerve at elbow (full anaesthesia)*

	Right hand (control)		Left hand (ulnar nerves injected)	
	Index	Little	Index	Little (anaesthetic)
Distal phalanx	17·8	15·3	18·8	12·8
Proximal phalanx	14·8	14·4	14·8	12·0
Metacarpal	13·5	13·4	13·6	10·6
Nail bed	—	—	11·5	9·5

These scale readings demonstrate a rise in temperature of 1 to 2° in the anaesthetic area (column 4). No temperature difference was detectable above the wrist, although anaesthetic.

But cooling of both limbs by immersion so increased the differences between the normal and the anaesthetic areas that the wrist area showed a rise of 2°, and the distal phalanx of the little finger a rise of 5°.

Exp. 16. *Superficial peroneal nerve*

Well-marked flush in anaesthetic area, but rise of temperature of only $\frac{1}{3}$°. After cooling by immersion, anaesthetic area was hotter than other foot by $1{\cdot}\frac{1}{3}$°.

Exp. 18. *Intercostal nerves, left,* 4, 5, *and* 6

No temperature changes.

N.B. In Exps. 12 and 15 the figures listed indicate scale readings. The lower readings mean higher temperatures. A difference of 3 in scale readings is equal to about 1° C. of temperature.

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THE HUMAN PINEAL GLAND AND PINEAL CYSTS

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INTRODUCTION

This investigation of the human pineal gland was stimulated by the fortunate collection of four pineal cysts. A complete study of the gland was made, from the second foetal month, through childhood to old age, in an endeavour to elucidate the origin of these cysts. From these observations an attempt will be made to show that cystic enlargement of the pineal may be an exaggeration of a normal occurrence rather than a pathological entity.

It is proposed to give a brief survey of the histology of the pineal, dealing first with the appearances during foetal life, then childhood, adolescence and each decade of adult life.

Fifty post-natal and seventeen foetal glands were examined.

DEVELOPMENT

The development of the human pineal has been thoroughly and admirably described by Krabbe (6), but a short résumé of the findings in the present research will be given in order to assist subsequent observations.

In the present series, the development of the human pineal gland was investigated in embryos ranging from 25 mm. crown-rump length to full term. Sections were all cut in the sagittal plane.

In the younger embryos the comparatively large anlage of the posterior commissure formed the chief factor in the orientation of the gland. This commissure was easily recognisable by its histological appearances.

In an embryo of 25 mm. length only a suggestion of a fold anterior to the small invagination of the posterior commissure represented the pineal gland (fig. 1). A little later, in an embryo of 30 mm. length, the anlage of the gland consisted of a backward hollow extension, the pineal diverticulum, of the roof of the hinder part of the diencephalon just in front of the anteriorly projected posterior commissure. In this embryo the anlage of the habenular commissure was discernible, the pineal fold lying between it and the posterior commissure.

At this stage the pineal anlage consisted of undifferentiated epithelial cells continuous with those forming the roof-plate of the diencephalon.

The features of the pineal in an embryo of 35 mm. were similar to those described and illustrated by Krabbe (6): a backward hollow extension from the roof of the third ventricle just anterior to the clearly demarcated posterior commissure, represented the posterior anlage, whilst adjacent and united to it was a mass of cells representing the anterior anlage (fig. 2).

Between the third and fourth months of intra-uterine life the anterior pineal anlage had increased in size and embraced the habenula. The pineal diverticulum, continuous with the third ventricle, was invested by the posterior anlage which joined the posterior commissure as this projected forwards into the ventricle. No line of demarcation between the cells of the two anlagen was discernible as described by Krabbe (6). Even at this stage the constriction of the diverticulum by the approximation of the two anlagen was noticeable (fig. 3).

In another example at this age, the gland appeared as a round mass of cells containing a cavity surrounded by tall columnar cells similar to those lining the diverticulum pineale. This cavity, or cavum pineale, was separated from the third ventricle by pineal cells. It was surmised that in this specimen the division of the diverticulum into cavum and recessus pineale had been effected (fig. 4).

Towards the middle of intra-uterine life, vascularisation of the pineal had commenced by a projection of vascular connective tissue into the periphery of the organ. Furthermore it was found that two types of cells were present; fine fibres and associated small cells, with pale nuclei containing one or two nucleoli, were believed to be neuroglial elements. The glial fibres ramified amongst the undifferentiated cells which were recognisable by their very deeply stained nuclei and small amount of cytoplasm. The neuroglial network of the posterior commissure was unmistakable and continued into the pineal mass. The connective tissue elements were distinguished by their elongated pale nuclei.

In sections from embryos during the later months of intra-uterine life, the architecture of the pineal was similar to that of post-natal glands. The recessus pineale, lined by ependyma, projected into the pineal anteriorly and was embraced by the neuroglial peduncles. Vascular connective tissue entered the periphery of the organ at many points, and the connective tissue septum originally separating the two pineal anlagen was observed. The neuroglial network of the pineal peduncles invaded the cellular mass and joined a similar network already present in the gland.

During the eighth foetal month the undifferentiated pineal cells had become transformed into the so-called pineal parenchyma. These cells were of much greater size, the pale nucleus, containing one or two nucleolar masses, being surrounded by a clearly defined hyaline or faintly granular mass of cytoplasm (fig. 5).

Infancy

During infancy the pineal was found to have assumed characteristics which persisted more or less throughout life. The parenchymatous mass fitted over the backward extension of the third ventricle, i.e. the pineal recess. The gland was prolonged forwards embracing the pineal recess and forming the pineal peduncles (fig. 6). A capsule derived from the pia mater enveloped the gland, and invaded it peripherally with fine blood vessels.

A neuroglial network was seen to form the peduncles and to insinuate itself

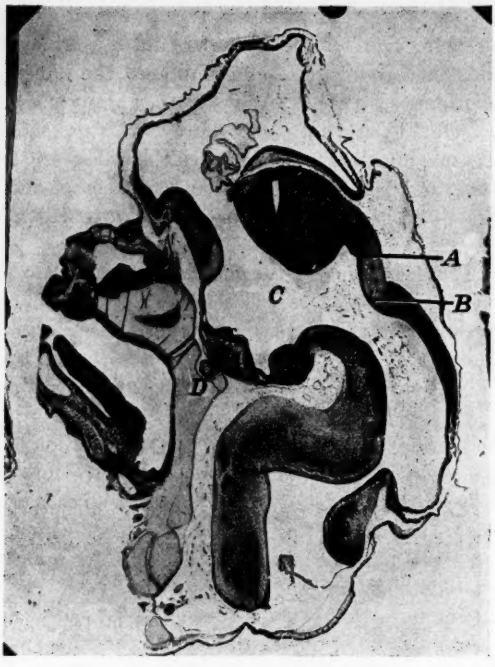

Fig. 1. Sagittal midline section through head of 25 mm. embryo. × 8. *A*, anlage of pineal gland in the form of a backward hollow extension. *B*, anlage of posterior commissure. *C*, third ventricle. *D*, pituitary body.

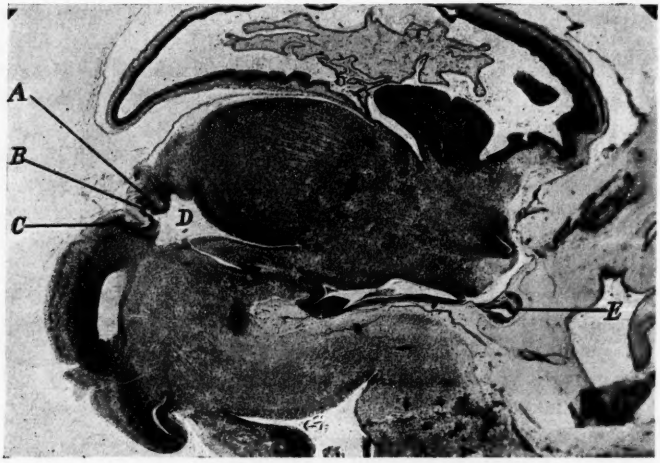

Fig. 2. Sagittal section through head of 35 mm. embryo, not quite median. × 10. *A*, anterior anlage of pineal. *B*, posterior anlage with diverticulum pineale. *C*, posterior commissure. *D*, third ventricle. *E*, pituitary body.

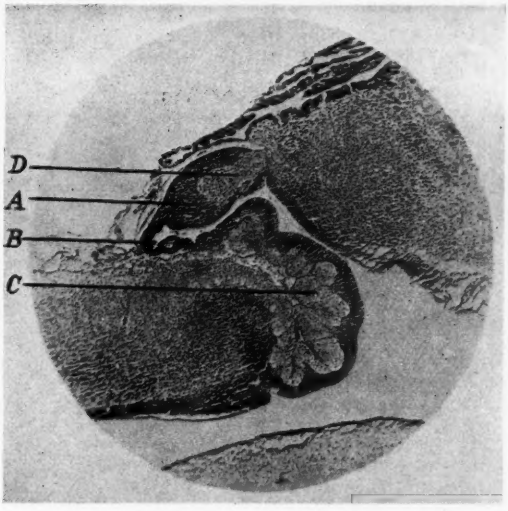

Fig. 3. Sagittal section through pineal region in embryo between the third and fourth months. × 35. *A*, anterior anlage of pineal. *B*, posterior anlage with pineal diverticulum. *C*, posterior commissure. *D*, habenular commissure.

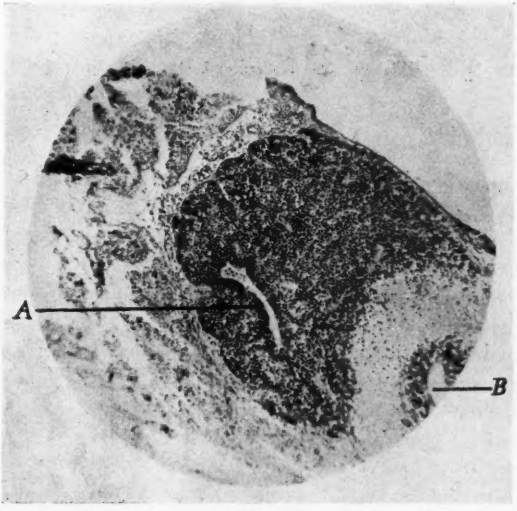

Fig. 4. Sagittal section through pineal region in a foetus of 4 months. × 60. *A*, cavum pineale. *B*, recessus pineale continuous with third ventricle.

as a band between the blind end of the pineal recess and the rest of the organ (fig. 6). From this band the glial network radiated throughout the gland, enmeshing the parenchymal cells (fig. 7). Furthermore a narrow glial band occupied the periphery of the pineal, separating the parenchyma from the pial capsule. The parenchymal cells were similar to those described as differentiating during the eighth month of foetal life (fig. 5). Mitotic changes were seen in the parenchymal cell nuclei in the infantile glands.

Four of the infantile specimens examined were "solid," in other words the cavum pineale was completely obliterated. In another case, from an infant aged 12 months, two small cavities were present in the gland. The larger one was surrounded by a wall of concentrically arranged glial fibres separating it from the parenchyma. The smaller one lay within the glial band adjacent to the blind end of the pineal recess. No cells were seen lining these cavities which were empty.

Within the "solid" glands mentioned above were one or two masses of glia devoid of parenchymal cells. These masses are known as "glial plaques," and it is suggested that they are formed during the constriction of the pineal diverticulum and the attempted obliteration of the pineal cave. It seems possible that glia is instrumental in closing the primitive cavities of the pineal.

Two specimens from infants aged 22 months presented variable features. One was "solid" and consisted of closely packed typical parenchymal cells enveloped in glial network. In the centre of the other specimen was a large oval cavity surrounded by a wide band of concentric glial fibres (fig. 8). The cavity was empty, but a few irregular cells were seen lining the mural glia. This appearance again suggests that glia plays an important part in the closure of the early pineal cave, but that the obliteration may be incomplete, leaving a cavity enveloped in glia. The original caval ependyma may disintegrate and disappear so that there is no cell lining to the cavities, but, on the other hand, some of these cells may persist. This important feature will be referred to again later.

Two specimens were obtained from children of 4 and 8 years and both were cavitated. The pineal from the child of 8 years contained four cavities, the largest lying in the long axis of the organ. It was enveloped by glial fibres within which a cellular lining was noticed.

Five examples of the pineal at puberty were examined. Each had distinctive features. All the glands had reached adult dimensions, the average antero-posterior diameter being 8·5 mm. One (13 years) contained a central cavity surrounded by a wide glial band. Lining the cavity distinct cells were observed. Posterior to the cavity were two irregular glial plaques. The rest of the organ consisted of typical glial meshwork and parenchyma.

Another pineal (12 years) had a very different appearance. The greater part of it was composed of large glial plaques, with glial network and parenchyma intervening. The parenchymal cells were considerably reduced in numbers, and each cell appeared to be isolated by glial fibres. A small cavity, devoid of cell

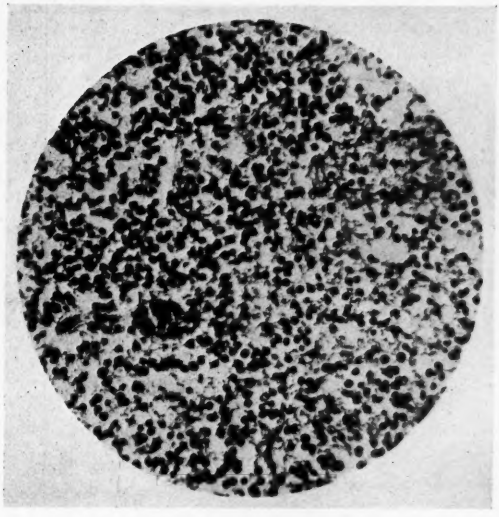

Fig. 5. Neuroglial network amongst pineal cells: full term. × 250.

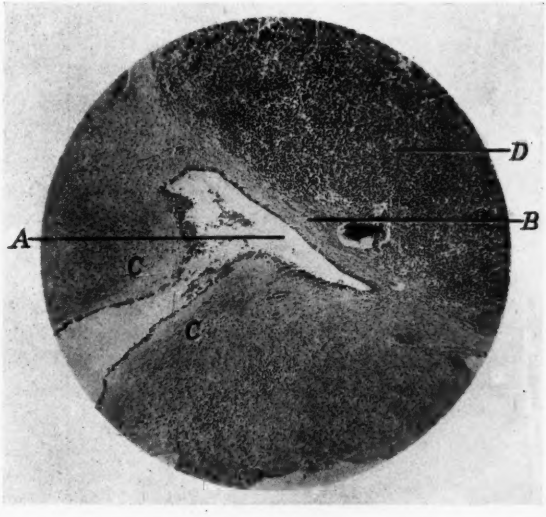

Fig. 6. Sagittal section of pineal of infant of 5 months. × 35. *A*, pineal recess lined by ependyma. *B*, strand of neuroglia. *C*, pineal peduncles. *D*, pineal mass.

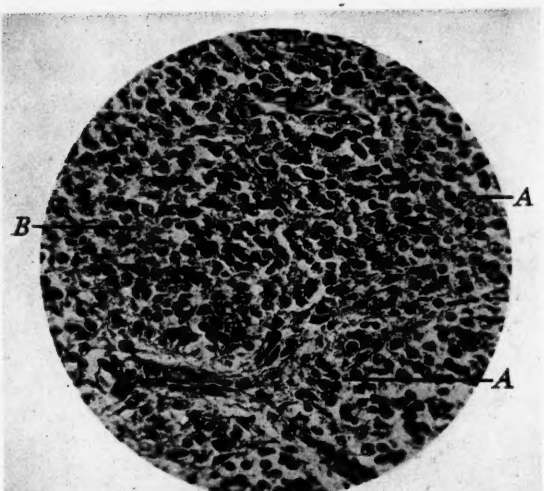

Fig. 7. Pineal parenchyma and neuroglial network. × 250. *A*, pineal cells with pale nuclei. *B*, neuroglial network.

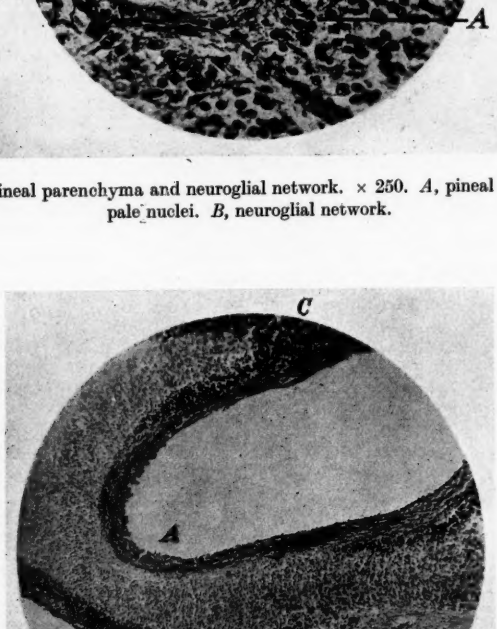

Fig. 8. Pineal of an infant aged 22 months. × 35. *A*, large cavity surrounded by concentric glia. *B*, pineal recess. *C*, pineal parenchyma. *D*, pineal peduncle.

lining, but containing cell débris, was situated within the largest glial plaque of this pineal.

The preponderance of glia at this age and the marked reduction in the amount of parenchyma seem to contradict the former belief that the pineal cells are gradually replaced by glia as age advances.

The third pineal of puberty (15 years) was similar. There was one very large glial plaque, and a smaller one containing a cavity. Within the latter were some lining cells and coagulated fluid. Adjacent to this plaque was a larger cavity, devoid of cells within, but occupied by coagulated material. A narrow glial band enveloped the larger cavity.

Of two pineals from subjects aged 15 years, one contained five cavities of variable size, each surrounded by thick glial walls, and into one was invaginated a small mass of pineal parenchyma. The other gland was composed of a solid mass of pineal cells and supporting glial network, devoid of cavities or glial plaques.

An interesting feature in these glands was the appearance of the so-called calcareous bodies. These had no relationship to blood vessels, but occurred irregularly amongst the pineal cells or glial plaques. They were similar in size to the cells. From careful observations it was thought that these structures originated in the cytoplasm of the parenchymal cells by a deposit of calcareous material, the cell later disintegrating and liberating the calcareous mass (fig. 9). Like calcareous deposits elsewhere, those in the pineal may represent a retrogressive change. It was found, however, that they were very numerous, though small, at puberty, occurred also in adjacent parts, and were absent in some of the adult glands.

Finally the specimens from individuals of 15 years showed commencing "loculation," but this appearance is more fully described below.

During the second decade many variations in the histology of the pineal body were encountered. The size was variable, the largest being fully a centimetre antero-posteriorly. Of the five specimens of this period examined, two contained cavities. In both cases the latter were surrounded by dense glial meshwork, and glial plaques also were observed. In none of the cavities were there any lining cells, but one contained cell débris. Small glial plaques were present in the remaining "solid" glands. Calcareous bodies occurred in all but one of this group. The number was variable; one gland contained such quantities in all parts that sectioning was extremely difficult, due to the hard stone-like property of the deposit after histological fixation.

At this stage "loculation" was definitely established. Radiations of glia pervaded the organs from glial plaques, but in addition, fibroglial strands divided the glands into loculi in which lay the parenchymal cells with the intervening glial network (fig. 10).

Of two glands of the third decade, one contained a very small cavity within a glial plaque, whilst in the other, four large cavities were discernible with the naked eye. A thick wall of concentric glial fibres encircled each cavity, but no

lining cells were present. The cavities, however, all contained coagulated material. The parenchyma and glial network called for no special description. There appeared to be no loculation in either case, whilst calcareous deposit was absent in one of the glands, and almost negligible in amount in the other.

The pineal bodies of the fourth decade conformed to type. Two of them contained a cavity enveloped by glia. In one case the cavity was large, but had no regular cellular lining, although many necrotic cells were observed around the periphery. In this gland small calcareous bodies were in process of formation.

In the other cavitated pineal from a subject aged 49 years, the space was surrounded by glia, and within this at one part was a definite row of cells lining the cavity.

Thirteen pineal bodies of the fifth decade were obtained. Of these seven were cavitated. Two contained five separate spaces, another four, another two, and the remaining organs each had one (fig. 11). The gland in which there were two cavities was interesting, because a tongue-like projection of glia and cells was invaginated into one of the spaces (fig. 12). Reference to this will be made later (p. 43). A wall of concentric glial fibres encircled all the cavities. In no case could any lining of cells be discerned.

It was difficult to understand why some of these organs contained so many cavities. It has been suggested that they are a degenerative change, but the regular arrangement of concentric glial fibres around them appears to be rather an attempt, albeit abortive, on the part of the glia to encircle, constrict and obliterate the original cavum pineale. In some cases the invasion of the cavum by neuroglia appears to be irregular, so that the cave is separated into compartments, each of which persists with concentric glia surrounding it, thus giving origin to multiple cavities. Furthermore it was found that calcareous masses never occurred within those cavities surrounded by concentric glia, indicating that their formation is not dependent on "brain sand" deposition (see p. 42).

Calcareous masses were present in all but three of these glands (fig. 13), and in some cases they were observed also in the pineal peduncles. The parenchyma and glia differed in no way from those at earlier periods of life. The cells appeared to be less numerous in some of these glands than in others, but this reduction may have been only apparent, depending on unavoidable post-mortem shrinkage, or slight variation in the thickness of the sections necessitated by the presence of "brain sand." Loculation occurred in the majority of the glands at this period of life.

Of the five pineal glands of the sixth and seventh decade, only one possessed a cavity surrounded by a glial wall. In all these cases were observed typical parenchymatous cells, glial network, loculation and calcareous deposits. The cells were present in considerable numbers in all the glands from aged individuals. This fact appears to throw doubt on the view(9) regarding the replacement of cells by glia in advancing age.

Four pineals from adults of uncertain age were included, since two of them

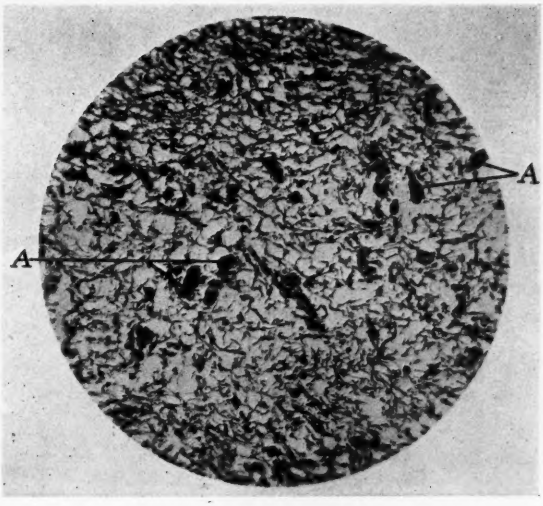

Fig. 9. Pineal gland at puberty showing formation of calcareous bodies (*A*) amongst neuroglial network. × 250.

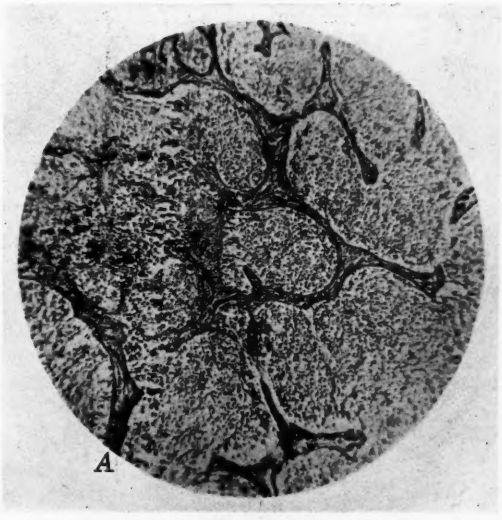

Fig. 10. Adult pineal showing loculation by fibroglial strands (*A*). × 60.

Fig. 11.

Fig. 12.

Fig. 11. Pineal of adult of 53 years showing many cavities surrounded by glial walls. × 35.

Fig. 12. Pineal during fifth decade showing tongue-like invagination into a cavity. × 12. *A*, cavities with glial walls. *B*, small glial plaque.

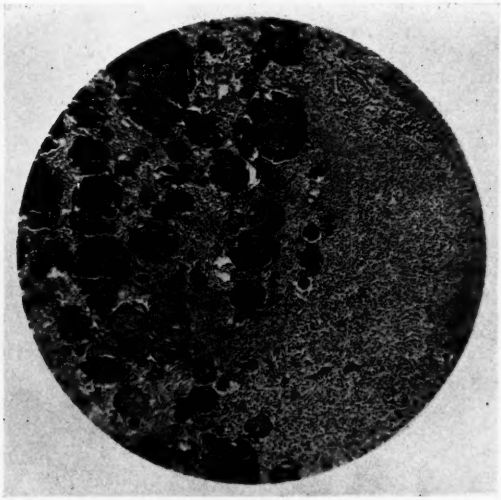

Fig. 13. Masses of "brain sand" in adult pineal. × 35.

each contained a very large cavity, enveloped by glia. Of great importance was the fact that distinct cells were observed lining the cavity inside the mural glia of the former case (fig. 14).

Three features were common to all pineal bodies examined. First a fibrous capsule was present, being derived from the pia mater and entering the periphery here and there with blood vessels. Secondly, the blood supply of this gland was extremely poor in comparison with that of such organs as the pituitary gland. Thirdly, the glia appeared to be similar in all cases. The individual glial cells consisted of a small triangular body apparently filled by a dark staining nucleus, and long delicate processes passing from the angles to envelop the parenchymal cells. With Cajal's gold sublimate technique these glial cells were demonstrated as astrocytes (fig. 15).

From this brief survey of the pineal gland at different stages of life, the following conclusions are drawn:

1. The human pineal is composed of typical parenchymal cells enmeshed in a neuroglial network. At birth the cells are characteristic. The glia appears during early foetal life, and the network amongst the parenchyma is observed about mid term, having spread from the original glia (described below). The organ increases in size until puberty when adult dimensions are reached. Parenchymal cell multiplication occurs during childhood.

2. The primitive diverticulum pineale is reduced to the recessus and cavum pineale during foetal life. It is suggested, contrary to the belief of Krabbe (6), that neuroglia might be responsible for the division of the diverticulum pineale. The primitive cells lining the diverticulum arise from embryonic spongioblasts (1), which are capable of developing into either ependyma or neuroglia. In this way, then, certain of the spongioblasts become neuroglial cells which appear to be instrumental in reducing the diverticulum and perhaps obliterating the cavum pineale.

In the present investigation, however, it has been seen that it is the exception rather than the rule for the cavum to be completely obliterated. In these cases it appears as though the glia had spread circularly around the cavum in an attempt to "squeeze it out," but had failed to do so completely, leaving a cavity, variable in size, surrounded by a wall of concentric glial fibres. The invasion by glia may be irregular so that the cavum pineale is divided into two or more compartments each of which becomes surrounded by glia and persists as a separate cavity.

In some cases, however, these particular spongioblasts may not all develop into glia, but some become what may be described as "pseudo-ependymal" cells. These line the cavity which has been surrounded by, but not obliterated by, glial fibres. The importance of these cells will be alluded to in the consideration of the pineal cysts. It is further suggested that, under some provocation, at present unknown, these "pseudo-ependymal" cells may be concerned with the outpouring of fluid into the cavity.

3. In cases where obliteration of the cavum pineale has been complete, glial

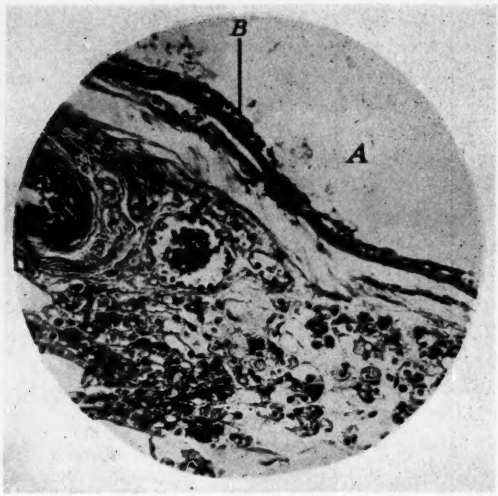

Fig. 14. Cells lining cavity in an adult pineal. × 250. *A*, cavity. *B*, lining cells.

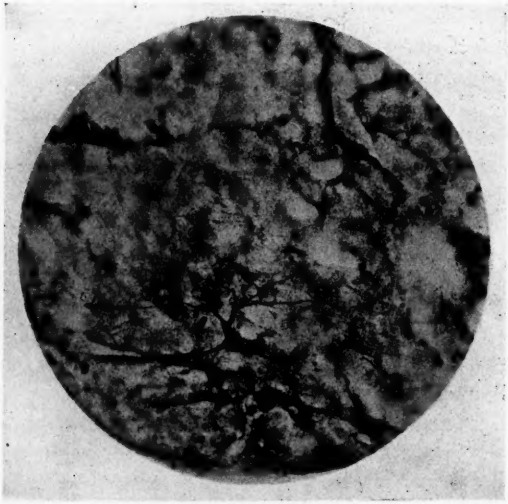

Fig. 15. Astrocytes demonstrated in an adult pineal body by Cajal's gold sublimate method. × 250.

plaques are prominent, but they are also present in cavitated glands. These plaques, however, may be either tangential sections through the mural glia of cavities, or obliterated portions of the primitive diverticulum pineale formed by the irregular invasion of it by glia.

The presence of glial plaques does not appear to be associated with old age, since the glands at puberty were found to contain the largest glial masses. Glia usually forms a peripheral band underneath the pial capsule and surrounds the pineal recess. The glia appears to belong to the astrocyte group.

4. "Loculation" of the pineal body by fibroglial trabeculae is present in most adult pineals. This may be part of the normal fibrosis consequent on advancing years, and is seen in other organs such as the pituitary body (3).

5. Calcareous bodies are discernible at puberty. It is suggested that they arise by a deposit of calcareous material within the parenchymatous cells which later disintegrate, freeing the mass. The small bodies later coalesce by further depositions on them.

6. The blood supply of the pineal body is not rich in comparison with that of the better known endocrine organs.

7. Judging from sections it appears as though the parenchymal cells were variable in numbers, but that a reduction is not necessarily associated with old age. Some organs at puberty were found to contain very few cells in comparison with glands from old people.

DISCUSSION

In the course of this investigation it has been observed that the cellular types in the human pineal gland are two in number: (*a*) parenchyma, and (*b*) neuroglia. This is in agreement with the findings of Hortega (5), although it has not been possible to demonstrate the finer details of the cells depicted in the admirable researches of this author. Krabbe (6), on the other hand, believes that nerve cells occur in the pineal, but this investigation has not revealed any.

The glia appears to belong to the astrocyte group, as has been shown also by Hortega (5). Although it has been fully described by many authors, so far no function has been assigned to it. Hortega (5) suggests that the important function of the pineal is localised in the parenchyma, and an accessory one in the glia. After careful investigation of this gland through all stages of life, it has been concluded that the glia differentiates during foetal life for the purpose of reducing the original pineal diverticulum. Krabbe (6) assigned this function to the parenchymal cells. Later, according to the present investigation, the glia is believed to be instrumental in an attempt to obliterate the pineal cave. In the majority of cases, however, the attempts are abortive, and a cavity, or cavities, persists.

There does not seem to be any doubt, judging from the present research and that of Krabbe (6), that the cavities represent the unobliterated distal part of the original pineal diverticulum. Furthermore the presence of such a cavity

serves as a foundation, in certain cases, for the production of cysts. On the other hand, Krabbe (6) believes that cavities in the pineal are a normal occurrence, and in later life tend to close spontaneously, but this is questionable on examination of the present series of adult pineal glands (see fig. 12). Marburg, quoted by Krabbe (6), suggests that the cavities may result from necrosis of a glial plaque. Judging from the present investigation this theory cannot be maintained as an explanation of cavity formation in the pineal, but it is suggested that "pseudo-cavities" may result from the deposition and coalescence of calcareous deposits which are lost during the histological technique. Such cavities are never surrounded by concentrically arranged glial fibres (see p. 36). Krabbe (6) also concludes that cavities are never produced by the destruction or degeneration of the parenchyma.

In the series under consideration, the wall of all cavities, irrespective of size, position, or age of individual, consisted of concentrically arranged glia devoid almost entirely of enmeshed parenchyma. Krabbe (6) found the walls to be composed of parenchymal cells at first, but during the second year a thin sheet of glia was noticeable between the parenchyma and the cavity. In old age he observed a thickening of the mural glia, the cavity in consequence becoming smaller. This was not found to be the case in the present series.

An observation, to which great importance is attached, is the presence, in an appreciable number of cases under investigation, of a clearly demarcated cell lining inside the mural glia of the cavities. For convenience these cells have been called "pseudo-ependymal" and suggestions as to their origin have already been made (see p. 41).

As far as could be ascertained from the available literature, only Krabbe and Marburg [quoted by Krabbe] (6) refer to any cells lying within pineal cavities. Krabbe (6) describes them as necrosing pineal cells, and calls them "ependymal-like" cells. Marburg (6) believes them to be true ependyma. Neither of these authors mentions any special arrangement of these cells within the cavities. In the series under consideration, cell débris was present in the cavities in several of the pineal glands, but in others, distinct healthy cells in a single layer were found around the periphery of the cavity (fig. 14).

The significance of this layer of cells is not thoroughly understood. The presence of coagulated fluid in certain of the cavities associated with a cell lining suggests that the cells may be concerned with the outpouring of fluid. Absence of coagulated material in many of the sections did not necessarily indicate that during life such material was not produced.

Reference must be made to the presence of glial plaques in the pineal gland. Judging from the present observations, it is believed that these are formed during the efforts of the neuroglia to obliterate the early pineal cave. Krabbe (6) believes them to be produced by proliferation of the mural glia of a cavity, or less likely, by the enlargement of the tractus pineale. His former suggestion is readily acceptable, and the irregularity of these plaques could be explained either by his or the author's theories.

Proliferation or hyperplasia of the glia has been seen to occur in the present series, and was particularly demonstrable in pineals at puberty. This proves almost conclusively that the hyperplasia is not dependent on, or concurrent with, advancing years. Furthermore in many pineal glands from aged individuals there did not appear to be any hyperplasia of the glia. Hortega (5) refers to the glial hyperplasia, but is unable to explain its initiation, as the amount is so variable, and the controlling factors are not known as yet. He found, however, that a number of diseases of the central nervous system were associated with an increase in the pineal glia. In the cases under investigation, there was nothing pathological in the central nervous system to explain the glial hyperplasia occurring in the two glands at puberty.

The significance of the lime concretions, or "brain sand," and the fibroglial strands in the pineal body is not yet fully understood. Krabbe (6) indicates that the former are related to nuclear excretion. In the present series, it was surmised that the lime salts were deposited in the parenchymal cells, which afterwards disintegrated and set free the calcareous mass. Formation of "brain sand" and "loculation" of the pineal by fibroglial strands may be retrogressive changes consequent on advancing age. A similar invasion by fibrous tissue occurs in the pars anterior of the pituitary body (3). Lord (7) many years ago referred to the loculation of the pineal body by trabeculae derived partly from the pial covering, and partly from the peduncles. In the present research, too, these strands were found to be composed of fibroglial tissue.

PINEAL CYSTS

Four pineal glands with cystic enlargement were examined. No statistics regarding the incidence, and very few descriptions of this condition, could be found in the available literature. It is certainly not a very frequent condition, although it is probably overlooked at autopsies on occasions.

Three of the cases obtained were from females, aged 42 years (A.), 42 years (B.), and 73 years (D.). The fourth was from a male of 38 years (C.). All of the specimens were removed from asylum patients: this fact may have been only coincidence or the condition may have influenced the mental history. Each pineal was considerably enlarged, D. measuring 13·5 mm. antero-posteriorly. In A., C. and D. the cystic enlargement was posterior, but in B. the main one was anterior and smaller ones lay behind it. The very large cyst in D. seemed to represent the coalescence of four smaller ones (fig. 16). The remaining parts of the glands were composed of typical parenchymal cells separated by glial fibres. The parenchyma was considerably reduced in all cases. Small glial plaques were noticeable in each gland.

All cavities, large and small, were encircled by a glial wall. In the larger cysts this was very attenuated and adjacent to and in contact with the pial covering.

In two cases A. and D. a tongue-like projection invaginated the cyst

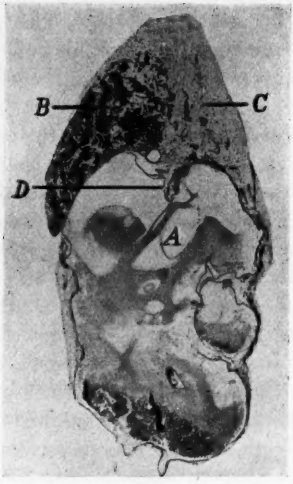

Fig. 16. Fig. 17.

Fig. 16. Pineal cyst from female aged 73 years. Case D. × 4. *A*, cyst containing coagulated material. *B*, pineal tissue. *C*, degenerated mass. *D*, tongue-like projection.

Fig. 17. Pineal cyst from female of 42 years (case A.), showing tongue-like projection into cyst (*A*). × 4.

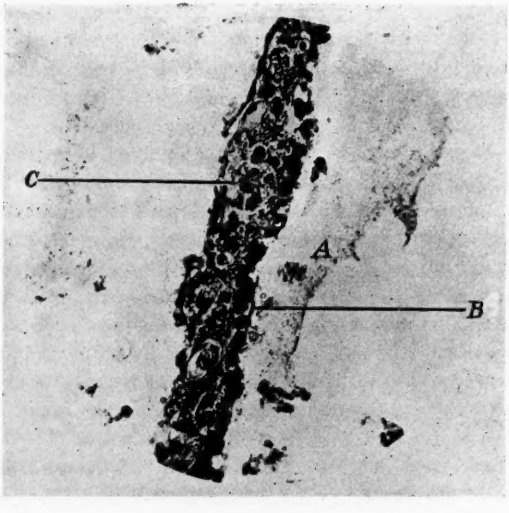

Fig. 18. Cells lining the cyst in case D. × 250. *A*, cavity of cyst. *B*, lining of cells. *C*, fibroglial wall of cyst.

anteriorly (fig. 17). A similar feature occurred in a normal pineal from a subject of 51 years (fig. 12: see p. 38).

The cysts in C. and D. contained hyaline material coagulated by histological fixation which prevented examination of the fluid. Careful investigation revealed the presence of a clearly defined layer of cells lining the larger cysts in each case. The cells were flattened, probably due to distension. In specimen D. the cyst was divided into four loculi by fine fibroglial strands (fig. 16). The cell lining was complete around each of the four compartments (fig. 18). In A., B. and C. the cell lining of the cysts was not quite complete, but this may have been due to autolysis.

In cases A. and C. the post-mortem examination revealed a flattening of the superior quadrigeminal bodies and a slight excess of cerebrospinal fluid. The foramina of Munro were widely patent and the cerebral ventricles slightly dilated. There were no autopsy reports of cases B. and D.

After careful consideration of the histories, post-mortem findings and histology, of the four cases of pineal cyst, it is suggested that in each case death resulted from increased intracranial pressure. This is readily explained by the intermittent pressure of the enlarged pineal body on the vein of Galen. As pointed out by Stopford (11), a small subtentorial enlargement, especially in the neighbourhood of the pineal gland, compresses the vein of Galen as it curves upwards around the splenium of the corpus callosum to join the straight sinus. This results in the onset of symptoms dependent on increased intracranial pressure.

The next point requiring elucidation is the cause of the cystic enlargement of the pineal body. Bearing in mind the fact that in the human pineal the cavum pineale persists more frequently than it is obliterated, the initial factor, i.e. the presence of a cavity, is evident. Presence of a cellular lining and fluid content in the cavity, in some of these cases, contributes a second factor, that is, a medium possibly concerned in the outpouring of fluid into the cavity. How these lining cells function in relation to the production of fluid cannot be explained with certainty at the moment.

The final factor, i.e. the initiation of outpouring of fluid into the cavity and its distension into a cyst is merely a matter of conjecture. It is suggested, tentatively, that some increase in the general venous pressure may be responsible, but the brief histories and the absence of full post-mortem findings in the four cases make it impossible to pursue this conjecture further.

Many years ago Stanley (10), Garrod (4), Russell (8), Campbell (2) and Lord (7), each described cases of cysts of the pineal which had come under their care. Only Campbell described the microscopic appearance. He found "a large cyst-like dilatation of the central cavity or ventricle of the pineal body. In places flattened cells could be seen along the inner lining of the cavity." Apparently all these cases were similar to those alluded to in the present research, but none of these authors was able to state how the cystic enlargement of the pineal was responsible for the death of their patients.

In conclusion, it is suggested that cyst-like enlargement of the human pineal body is an exaggeration of a normal occurrence, but it cannot be stated dogmatically what factor is concerned in the initiation of the enlargement.

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I wish to express my thanks to Prof. Stopford, of the Anatomy Department of the University of Manchester, for his kind help and valued criticism; to Dr R. Handley, of the County Mental Hospital, Prestwich, for providing me with three pineal cysts, histories of the patients, and also some normal glands; to Dr Dawson, Dr Susman, Dr D. Sheehan and Dr Henderson for many excellent specimens; to Mr H. Gooding, histologist in my department, for his skill and care in preparing the photographs.

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THE BUSHMAN BRAIN

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INTRODUCTION

The anthropology of the brain, as Ariëns Kappers indicates (1), is a subject which is worthy of being elevated from its present state of neglect. The present investigation was inspired by Woollard's paper on the Australian brain (2). Further grounds for recording this enquiry are the paucity of knowledge concerning the brain of this most interesting race, and the inevitability that such brains will become more and more difficult to procure. All that is known of the brain in Bushmen and Hottentots is represented by the papers of Tiedemann, Marshall, Koch, Sergi and Rawitz.

THE MATERIAL

The material available in the Anatomy Department of the University of Cape Town consists of two complete brains of Bushmen and one half-brain of a Bushwoman. These are the only brains from Bushman types met with in a series of almost 900 cadavers mostly native and coloured. All the brains were preserved in 10 % formalin.

Brain 1. This is a complete brain of a male, whose age was said to be 108. This specimen unfortunately presents a certain amount of hydrocephalus. Further the right hemisphere of the cerebrum is markedly smaller than the left. In the cerebellum the right lobe is slightly larger than the left.

Brain 2. Left half of brain of a female. This specimen is exceptionally small (*v.i.*).

Brain 3. Complete brain of male. Age 34. Left hemisphere of cerebrum is slightly longer than right. Right lobe of cerebellum larger than left. The veins of this brain were exceptionally well shown and consequently produced marked indentations on the surface of the brain. The arachnoid and pia mater were also very closely adherent to the brain surface.

This investigation falls naturally into two sections:

A. Description of various features—Encephalology.

B. Measurement of certain data—Encephalometry.

A. ENCEPHALOLOGY

I. General description

All three brains are small as compared with normal European brains, brain 2 being particularly diminutive. This is in keeping with the general smallness of Bushman body features. The parietal eminences are particularly well-marked in brain 3.

The Sylvian region and the insula. Exposure of the insula

The insula is exposed in both hemispheres of brain 1, and in both hemispheres of brain 3, but not in brain 2.

In brain 1 the exposure is more marked on the right hemisphere, and in brain 3 the exposure in both cases is mainly at the anterior extremity. In these two brains the exposure is due to defective orbital and frontal opercula.

Anterior rami of lateral fissure

The anterior rami of the lateral fissure are very variable. Both rami definitely emerge from the fossa in only three out of the five hemispheres, for in the left hemisphere of brain 1 the anterior ascending ramus is not shown definitely, and in the left hemisphere of brain 3 the anterior horizontal is very short and does not completely emerge from the fossa.

The two rami emerge in a common stem in the right hemispheres of brains 1 and 3, thus enclosing a V-shaped frontal operculum between them. In brain 2 the two rami come out of the fossa separately. The anterior ascending ramus runs slightly backwards as well as upwards so that we have a wide interval between the two, which is divided by a little sulcus into two more or less equal parts.

Gyri breves and gyrus longus

In the three hemispheres of brains 1 and 2 some of the gyri breves are almost equal to the gyrus longus in length. Several gyri breves join each other.

In both hemispheres of brain 3 the gyri breves unite at their lateral extremities to form a gyrus which is parallel to the gyrus longus. In this brain the insula is comparatively large, especially anteriorly.

Temporal area

Acoustic gyri. (*Transverse temporal gyri of Heschl.*) In the right hemisphere of brain 1, in brain 2 and in the right hemisphere of brain 3, the sulcus between these two gyri is deficient medially, where the gyri therefore fuse.

In the left hemisphere of brain 3 they fuse laterally.

Only in one hemisphere, therefore, viz. the left hemisphere of brain 1, are the two gyri definitely marked off from each other along their whole length. In the right hemisphere of brain 3 the anterior gyrus is larger than the posterior.

With the exception of the left hemisphere of brain 3 there is no sulcus or indentation separating the acoustic gyri from the lateral surface of the superior temporal gyrus in any of the hemispheres. In the one exception the two gyri are separated from that surface of the superior temporal gyrus by a sulcus which extends posteriorly on to the superior surface of the temporal lobe, i.e. the surface in the lateral fossa of Sylvius.

Superior temporal sulcus and gyrus. In two hemispheres (right of brain 1 and right of brain 3) the superior temporal sulcus is not interrupted super-

ficially (i.e. it is interrupted only by sunken gyri). In the remaining three hemispheres, the sulcus is completely interrupted into two parts, in addition to the presence of sunken gyri. In these cases therefore the superior temporal gyrus unites with the middle temporal gyrus.

Width of the superior temporal gyrus. Woollard (2) records a marked reduction in the width of the superior temporal gyrus in one of his Australian brains. The same reduction is seen in brain 3 of this collection of Bushman brains.

Width about middle of posterior ramus of lateral fissure (in mm.)

	Brain 1	Brain 2	Brain 3
Right hemispheres	14	—	6
Left hemispheres	13	15	8

Middle temporal sulcus. This sulcus is in two definite parts in four hemispheres of the five (all except brain 2).

In the left hemisphere of brain 1 the anterior part joins the superior temporal sulcus.

In the right hemisphere of brain 3, the larger anterior part runs right to the temporal pole, and the smaller posterior part runs obliquely upwards to terminate close to the superior temporal sulcus, to which it is joined by a deep indentation caused by a vein.

In brain 2 this sulcus is continuous in its whole length except for a very small anterior part at the temporal pole.

Inferior temporal sulcus. This sulcus is continuous in three hemispheres (brains 1 and 2). In all three cases the anterior ends are more or less parallel to the rhinal fissure. In both hemispheres of brain 1, the sulcus terminates posteriorly by turning over the inferolateral border to the superolateral surface.

In brain 2 it is joined posteriorly by the collateral sulcus.

In both hemispheres of brain 3 the inferior temporal sulcus is interrupted into two parts at about its middle. In both hemispheres, the posterior part is more or less parallel to the collateral fissure; but whereas the anterior part in the right hemisphere is more or less parallel to the rhinal fissure and gives off a little sulcus to join it, in the left hemisphere the anterior part converges on the rhinal fissure and terminates in close proximity to it.

The posterior extremity of the posterior part in the right hemisphere and the anterior extremity of the posterior part in the left hemisphere present bifurcations, the upper limbs of which both turn round the inferolateral border to the superolateral surface.

Rhinal and collateral sulci. The collateral sulcus does not join the rhinal fissure in any one of the hemispheres. In brain 2 it joins the inferior temporal sulcus. In the right hemisphere of brain 3 the rhinal fissure is connected to the anterior part of the inferior temporal sulcus by a communicating sulcus.

The *uncus* is very prominent in all three brains.

(In brain 1 the isthmus of the gyrus fornicatus presents a well-marked elevation. This is in all probability due to the brain substance being pushed over the edge of the tentorium cerebelli. The condition of hydrocephalus is responsible for the expansion of third and lateral ventricles, the attenuation of the substance of the corpus callosum and its increase in length, the displacement of the fornix from the corpus callosum right from the splenium and the consequent great increase in extent of the septum pellucidum.)

Size of temporal lobe. In all three brains, the temporal lobe appears to be small on the whole. In brain 3 it is noticeably smaller on the right than on the left hemisphere.

Occipital region

Calcarine fissure and sulcus lunatus. The anterior and posterior calcarine fissures are well shown in all the brains. The lateral calcarine sulcus is only typically present in the two cases in which the sulcus lunatus is typical or almost typical, viz. left hemispheres of brains 1 and 2. In both these cases, however, the lateral calcarine sulcus is interrupted before it terminates by being surrounded by a sulcus lunatus.

In the other three hemispheres, atypical lateral calcarine and lunate sulci may be made out by piecing together irregular sulci.

The *sulcus lunatus* is typical in only one out of the five hemispheres—brain 2. It is almost typical in the left hemisphere of brain 1 (*v.i.*).

The *sulci limitans superior and inferior and the sulcus sagittalis lingualis* are present in some form or other in all the hemispheres.

The *sulcus paracalcarinus and the arcus intercuneatus* do not present any consistent features.

The *sulcus praelunatus* extends forwards irregularly from the sulcus lunatus (typical and atypical) to end either in close proximity to or actually in connection with the anterior occipital sulcus, the sulcus angularis, and so to the termination of the superior temporal sulcus.

The *occipital poles* of the right hemisphere of brain 1 and both hemispheres of brain 3 present well-marked depressions due to the superior sagittal blood sinus.

Parietal region

Sulcus centralis: junction with lateral fissure of Sylvius. In two out of the five hemispheres (viz. in the left hemispheres of brains 1 and 2) the sulcus centralis joins the lateral fissure directly. In the remaining three hemispheres the only connection is an indirect one—through the sulcus subcentralis anterior. In fact, in the right hemisphere of brain 1, there is no actual junction with the sulcus subcentralis anterior. In the right hemisphere of brain 3, the central sulcus is connected to the sulcus subcentralis anterior just by a shallow sulcus, and in the left hemisphere of this brain, where this junction is more definite, the sulcus subcentralis anterior does not completely join the Sylvian fissure.

Relation to superomesial border. The sulcus centralis cuts the superomesial border and extends on to the medial surface for about ½ inch in four out of the five hemispheres. In the one exception, viz. the right hemisphere of brain 3, it does not even reach the superomesial border.

The *paracentral lobule* is well defined in all the hemispheres except the left one of brain 1, where the sulcus paracentralis is defective.

Sulcus intraparietalis proprius. This sulcus joins the postcentral sulcus in all five hemispheres. The four genetically distinct parts of this sulcus fused superficially and were divided only deeply by annectant gyri in both hemispheres of brain 1 and in brain 2. In brain 3 this sulcus is split up into two parts in the right hemisphere (one parietal and one occipital) and three parts in the left hemisphere (two parietal and one occipital).

Frontal region

The striking feature of this region in these brains is the highly convoluted appearance due to the large number of small irregularly disposed gyri.

Precentral sulcus. The superior and inferior precentral sulci are confluent in only two hemispheres—the two of brain 1. In no hemisphere is this sulcus directly continuous with the lateral fissure of Sylvius. In the right hemisphere of brain 1, it is connected by a shallow groove to the sulcus subcentralis anterior and hence indirectly to the Sylvian fissure. In the right hemisphere of brain 3, the precentral sulcus is joined to the fissure of Sylvius by the sulcus subcentralis anterior, and in the left hemisphere of brain 3, the precentral sulcus is joined to the central sulcus of Rolando by a shallow transverse connecting sulcus.

The sulcus precentralis medius is separate from the sulcus precentralis superior in only one hemisphere, viz. the right hemisphere of brain 3, but even in this case they are very close to each other and seem to join when looked at casually. It should be noted also that in brain 2 there is a small sulcus above the superior precentral, which cuts the superomedial border and extends for about ½ inch on both the medial and superolateral surfaces.

Sulcus subcentralis anterior. This little sulcus is present in all cases except in brain 2.

The *sulcus radiatus of Eberstaller* seems to be present in all five hemispheres, as also is the *sulcus frontomarginalis.*

Superior frontal sulcus. This sulcus is continuous almost to the frontal pole in four of the five hemispheres studied. In the one exception, viz. the right hemisphere of brain 3, it is interrupted into a longer posterior part and a shorter anterior part.

It is directly continuous with the superior precentral sulcus in all the hemispheres except the left one of brain 1. (In the right hemisphere of brain 3 it is continuous with the sulcus precentralis medius.)

The superior frontal sulcus terminates by joining the frontomarginal sulcus in only one case—brain 2.

Sulcus frontalis medius. This sulcus is completely absent in brain 2, and in brain 1 is only represented by a number of irregular little sulci. In brain 3 it is present in both hemispheres but interrupted into a well-defined longer posterior part which is not continuous with the precentral sulcus and an irregular anterior part which fuses with the frontomarginal sulcus.

Superior frontal gyrus and lateral and medial paramesial sulci. The lateral and medial paramesial sulci which divide the superior frontal gyrus into two parts on superolateral and medial surfaces respectively are best shown in brain 2, where they are represented by short continuous longitudinal furrows running parallel to the superomedial border. The medial paramesial is the smaller of the two. In both hemispheres of brain 1 and both hemispheres of brain 3, these sulci are represented only by a large number of irregularly disposed little sulci on both the lateral and medial surfaces.

Sulcus cinguli and gyrus cinguli. This sulcus is present in its normal form in all cases except brain 2 where it is interrupted by a small gap anteriorly. From this point anteriorly the gyrus cinguli is divided longitudinally into two parts by a small sulcus parallel to the curved part of the sulcus cinguli. (In brain 1, the gyrus cinguli is very narrow, due to the hydrocephalus.)

II. Special features which have been used as criteria for comparison

Narrow width of frontal lobes (or rather pronounced parietal width). This feature which is conspicuous in both Marshall's and Koch's Bushwomen's brains (Kappers (1)) is also well shown in the present collection, particularly in brain 3. This is in keeping with the characteristic shape of the Bushman cranium.

Frontal and occipital flatness, as shown by Marshall's brain, is also manifest in this series, particularly in brain 2 (which seems to be the most primitive brain). There is also a tendency to a "*square-cut*" *contour at the occipital end,* particularly in brains 2 and 3—a feature which Duckworth (3) says appears in lowly human brains and in brains of gorillas and other Simiidae and which he found distinct in one hemisphere of his Australian brains.

Gyration. Like Koch's Bushwoman's brain, the present series display strong gyration, the frontal lobe being particularly highly convoluted.

In no case are the convolutions infantile and lacking the fulness of complexity (a feature of Bushman brains recorded by Duckworth (4)), although there is a tendency in this direction in brain 2.

Rostrum orbitale. This feature, regarded by Duckworth (3) as a Simian characteristic, is particularly well shown in brain 3, less so in brain 2 and still less so in brain 1. In fact only in brain 3 can it be said to exceed the normal. Koch found it particularly pronounced in his Bushwoman's brain. Kappers (1) found this also in Neanderthal endocranial casts.

Anastomosis of ramus posterior of lateral fissure with superior temporal sulcus. This feature which may be considered primitive (Kappers (1)) is shown in

Sergi's Hottentot brain and also occasionally in Hereros. It is not shown in any of the present series.

Continuity of sulcus frontalis medius. This is regarded as a primitive feature. Sergi found this sulcus more frequently continuous in Hereros than in Europeans, and Kappers observed this also in palaeolithic brains, viz. Neanderthal endocranial casts. In the present collection this sulcus is present with any degree of continuity only in brain 3. In fact it is completely absent in brain 2.

Curvature of the rhinal fissure. A boldly curved rhinal fissure is according to Duckworth (3) evidence of lowly affinities. Duckworth (3) and Woollard (2) each found this feature once in their Australian brains. In this present collection of Bushman brains, this fissure is boldly curved only in brain 2 and slightly so in three other hemispheres.

Exposure of the insula. This character, regarded by Woollard and Duckworth as a distinctive feature of the Australian aboriginal brain, is well shown in these Bushman brains, being present in four hemispheres out of five (all except brain 2).

Discontinuity of sulcus intraparietalis proprius. Duckworth (3) considers this a primitive feature, particularly the separation of this sulcus from the postcentral sulcus. In this present collection, the sulcus intraparietalis proprius is joined to the postcentral sulcus in all five hemispheres, and is completely continuous in three hemispheres out of five.

Retrocalcarine fissure and sulcus lunatus. The importance of these sulci has been shown by Elliot Smith, and Woollard goes so far as to state that "in the identification of these fissures, Elliot Smith has discovered so far the only reliable criterion of a primitive human brain."

Woollard (2) concludes that the primitive condition of these fissures is present in practically all pure-blooded Australian aboriginals and Shellshear (4) found a similar primitive arrangement in the occipital area of Chinese brains. In the present collection of Bushman brains, the perfectly typical condition of these sulci is found in only one hemisphere, although it is practically typical and easily identifiable in one other hemisphere.

B. ENCEPHALOMETRY

Introductory note

The use of measurements of the brain as criteria of comparison cannot be claimed to be on a definite stable scientific basis as long as there are no fixed universal standards in use with regard to the nature and strength of the preservative solution, the duration of preservation and the time of drying before measurement. Variations in these important factors no doubt cause discrepancies in the results obtained. It is therefore to be hoped that before long international standards will be established and adopted by all investigators.

The present collection of brains was preserved in 10 per cent. formalin. Before being weighed, each brain was allowed to drain for 20–30 minutes.

I. *Weights*

		Total brain gm.	Right hemisphere of cerebrum gm.	Left hemisphere of cerebrum gm.
Brain 1		965	381	456
Brain 2	Half	425	—	362
	Whole	850 approx.		
Brain 3		1097	480	471

From the above figures it is clear that the Bushman brain has (as one would expect from its small size) an exceedingly small weight. For comparison we may cite Woollard's figures for three Australian brains: 1138·0, 1123·0, and 1044·6 gm., and Kappers' average figure for Southern Chinese brains—1239 gm., and for Dutch males 1322 gm. Villiger (6) gives the following list of average weights for different races:

Caucasian	1335 gm.
Chinese	1332 ,,
Sandwich Islander	1303 ,,
Malay and Indian	1266 ,,
Negro	1244 ,,
Australian	1185 ,,

It is of interest to note that Kappers determines from Pittard's figures for the capacity of the Bushman-Hottentot cranium that the average brain weight for males is 1343 gm. and for females 1196 gm. He records that Sergi's Hottentot brain weighed 1201 gm., and in a footnote states that the reported weights of Marshall's and Koch's Bushwomen's brains (872 and 844 gm. respectively) are "too small." The value of this statement is greatly diminished by the fact that brain 2 (the only female of this series) has an approximate weight of 850 gm. (*vide supra*). Furthermore, the average of the two male brains (1031 gm.) is also well below the figure given by Kappers for male Bushmen (1343 gm.).

Indubitably, therefore, the weight of the Bushman brain is lower than that of any other living race of Man as yet recorded.

II. *Indices*

$$\text{Brain index} \frac{\text{Greatest diameter}}{\text{Greatest length}}$$

		Greatest diameter mm.	Greatest length mm.	Brain index
Brain 1		118	174	67·82
Brain 2	Half	52	145	(71·72)
	Whole	104 approx.		
Brain 3		114	166	68·67
			Mean	69·40

This index therefore shows a high degree of dolichocephaly, very much greater than that shown by Woollard's Australian brains (average 73·27) and Kappers' Dutch brains (75·2–80·3).

Following Kappers' suggestion, the remaining indices were calculated from measurements taken on photographs of the brains. In determining the frontal height and frontal length indices, I have used his more recent system involving the chiasma perpendicular, as set forth in *The Evolution of the Nervous System in Invertebrates, Vertebrates, and Man* (1929). A full description of the way in which the various lines are drawn, measurements taken, and indices calculated, may be obtained from that volume.

		General height index	Occipital index	Temporal depth index
Brain 1:	Right hemisphere	0·539	1·237	0·132
	Left ,,	0·470	1·121	0·167
Brain 2:	Left ,,	0·538	1·271	0·154
Brain 3:	Right ,,	0·506	1·174	0·138
	Left ,,	0·508	1·209	0·122
	Mean	0·512	1·202	0·143

		Temporal length index	Frontal length index	Frontal height index	Callosum index
Brain 1:	Right hemisphere	0·742	0·348	0·494	0·325
	Left ,,	0·744	0·327	0·414	0·335
Brain 2:	Left ,,	0·771	0·290	0·473	0·319
Brain 3:	Right ,,	0·744	0·316	0·459	0·327
	Left ,,	0·734	0·364	0·464	0·312
	Mean	0·747	0·329	0·461	0·324

General height index (0·512)

A very impressive fact is that in spite of the hyperdolichocephaly of these Bushman brains, the general height index is higher than those of Marshall's Bushwoman (0·469), of Kappers' dolichocephalic Dutchmen (0·491) and of Woollard's Australians (0·502) and approaches more nearly that of Kappers' brachycephalic Dutchmen (0·522). The Chinese brain has a still greater height index (0·535) which approaches nearest to the foetal figure (0·586).

It should be noted that the mean value of the general height index of the present collection is lowered particularly by the comparatively low value of this index in one of the five hemispheres, viz. the left hemisphere of brain 1 (0·470).

Occipital index (1·202)

This index is larger in the present collection than in Woollard's collection of Australian brains (1·008), indicating a steeper occipital slope. Marshall's Bushwoman's brain has an occipital index of 1·275—very slightly higher than that of the present collection to which the average value for Dutch dolichocephalics is almost equal (1·190). All these values are however considerably

below the figures for Dutch brachycephalics (1·45), foetuses and neonati (1·47) and Chinese (1·56), brains of which have therefore much steeper occipital slopes. It should be noted again that in the left hemisphere of brain 1 this index is considerably lower than the remaining four figures.

Temporal depth index (0·143)

This index does not show any marked difference from the values obtained for Marshall's Bushwoman (0·137) or for Dutch dolichocephalics (0·145). It is however definitely larger than the figure for Woollard's Australians (0·127), indicating a relatively wider temporal area and smaller than the figures for Dutch brachycephalics (0·160), foetuses (0·157) and Chinese (0·166), indicating a relatively narrower temporal area.

The left hemisphere of brain 1 shows a very high temporal depth index (0·167) and the left hemisphere of brain 3 a particularly low one (0·122).

Temporal length index (0·747)

The relative length of the temporal area as indicated by this index is almost equal to that of Dutch dolichocephalics (0·748). It is relatively slightly shorter than the temporal area of Marshall's Bushwoman's brain (0·755) and still more so than that of Dutch brachycephalics (0·760) and Chinese (0·780). The lowest value in the present series is that of the left hemisphere of brain 3 (0·734), which coupled with its very low temporal depth index (*vide supra*) gives this hemisphere the relatively smallest temporal area.

Frontal length index (0·329)

This is considerably less than the corresponding figure for Marshall's Bushwoman (0·362), Kappers' Australian cast (0·356), dolichocephalic Dutch (0·346), brachycephalic Dutch (0·363) and Chinese (0·343). Interesting is the fact that the nearest values are those for foetuses and neonati (0·326) and for Rhodesian man (0·332?). One would therefore conclude that these Bushman brains present a relatively shorter frontal area. It should be noted however that the average is lowered considerably by the particularly low value for brain 2 (0·290), which appears to be the most primitive brain of this series (*vide supra*).

Frontal height index (0·461)

As compared with the corresponding figures for Marshall's Bushwoman (0·408), Kappers' Australian cast (0·426) and dolichocephalic Dutch (0·443), this index is comparatively high and therefore indicative of a relatively larger frontal height. It is however lower than the index for Dutch brachycephalics (0·473), foetuses (0·503) and Chinese (0·470).

Again it must be pointed out that in the left hemisphere of brain 1 (the most dolichocephalic of the hemispheres) this index is very low (0·414) and is very high in the right hemisphere of the same brain (0·494).

Callosum index (0·324)

This index is of the same order of magnitude as the corresponding indices for Marshall's Bushwoman's brain (0·320) and for dolichocephalic Dutch brains (0·321). All these three are greater (indicating a relatively higher corpus callosum) than the figure for Woollard's Australians (0·310), but are considerably smaller than the corresponding indices for brachycephalic Dutch (0·382), Chinese (0·383) and foetuses (0·402).

The lowest value for the present series is given by the left hemisphere of brain 3 (0·312).

III. *Sylvian and Rolandic angles*

These were also measured, using Kappers' system:

		Sylvian angle	Rolandic angle
Brain 1:	Right hemisphere	61°	23°
	Left ,,	62°	25°
Brain 2:	Left ,,	66·5°	26°
Brain 3:	Right ,,	59·5°	29°
	Left ,,	62°	24°

IV *Depth of fissures*

As a certain amount of importance has been attached to the depths of fissures, some of the more important ones were measured, viz.:

		Parieto-occipital sulcus mm.	Calcarine fissure mm.	Central sulcus mm.	Intraparietal sulcus mm.
Brain 1:	Right hemisphere	20	18	18	19
	Left ,,	21	15	20·5	19
Brain 2:	Left ,,	16·5	21	24	22
Brain 3:	Right ,,	22	18	21	21
	Left ,,	23	19	21	22

An interesting fact which emerges is that the calcarine fissure is deepest and the parieto-occipital sulcus shallowest in brain 2, which has been regarded as the most primitive brain of the series (*vide supra*).

The intraparietal sulcus is consistently neither deeper nor shallower than the central sulcus, the mean values being 20·6 and 20·9 mm. respectively. Duckworth (3) found the intraparietal deeper than the central sulcus in Australian brains, as also did Cunningham (7) in Anthropoids.

SUMMARY

1. The most outstanding so-called primitive feature which appears constantly in these brains is the exposure of the insula.

2. There is a tendency towards other primitive features shown particularly well in one or two of the five hemispheres, but not consistently in all, viz. pronounced rostrum orbitale, curvature of the rhinal fissure, retention of the sulcus lunatus.

3. The general appearance and proportions are such as one would expect

from the characteristic configuration of the Bushman cranium, e.g. pronounced parietal width, frontal and occipital flatness.

4. There is a high degree of dolichocephaly.

5. The total brain weights and the weights of the hemispheres are very small, being lower than that of any other living race recorded.

ACKNOWLEDGMENTS

My thanks are due to Prof. M. R. Drennan for his guidance, criticism and advice, and to Mr A. A. Lamb for his assistance, particularly as photographer.

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EXPLANATION OF PLATES I TO V

Plate I

Brain 1. Lateral and medial aspects of right hemisphere.

Plate II

Brain 1. Lateral and medial aspects of left hemisphere.

Plate III

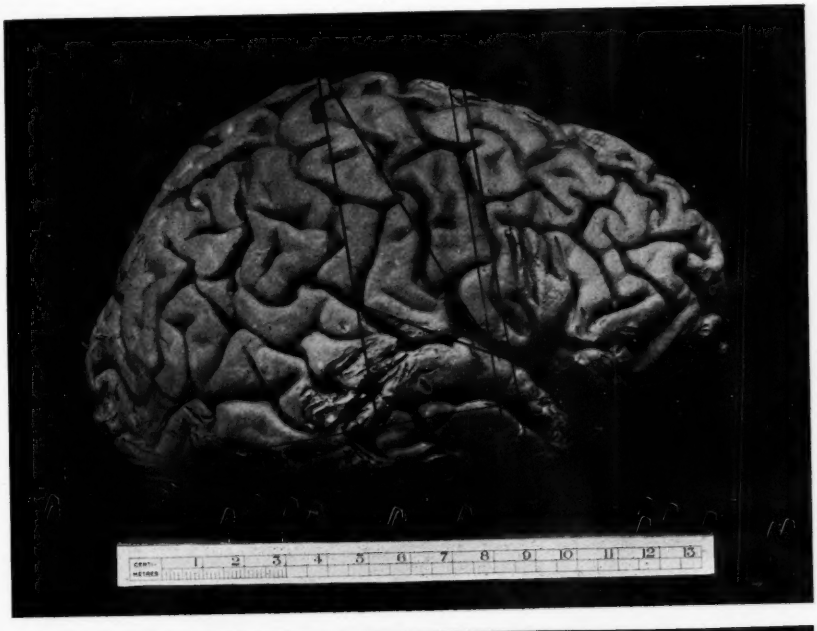
Brain 2. Lateral and medial aspects of left hemisphere.

Plate IV

Brain 3. Lateral and medial aspects of right hemisphere.

Plate V

Brain 3. Lateral and medial aspects of left hemisphere.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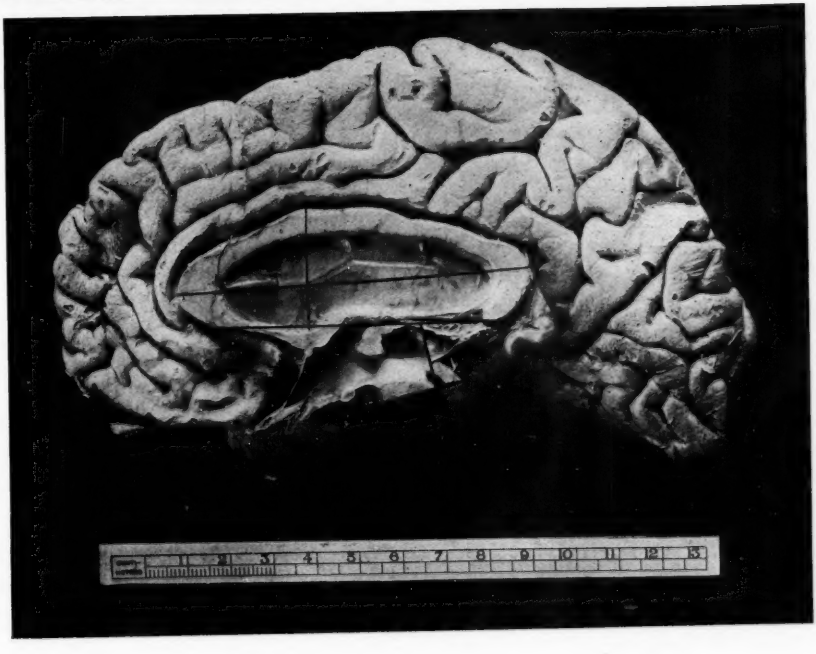
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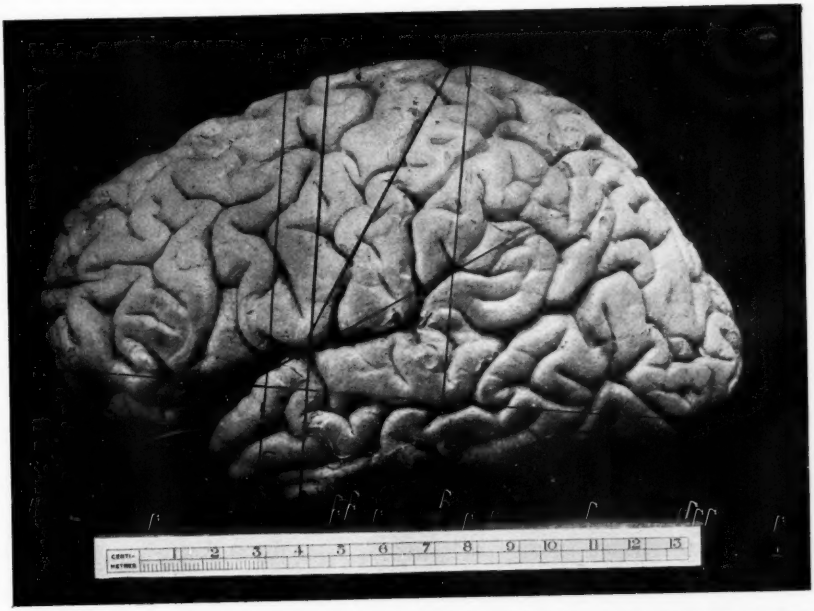
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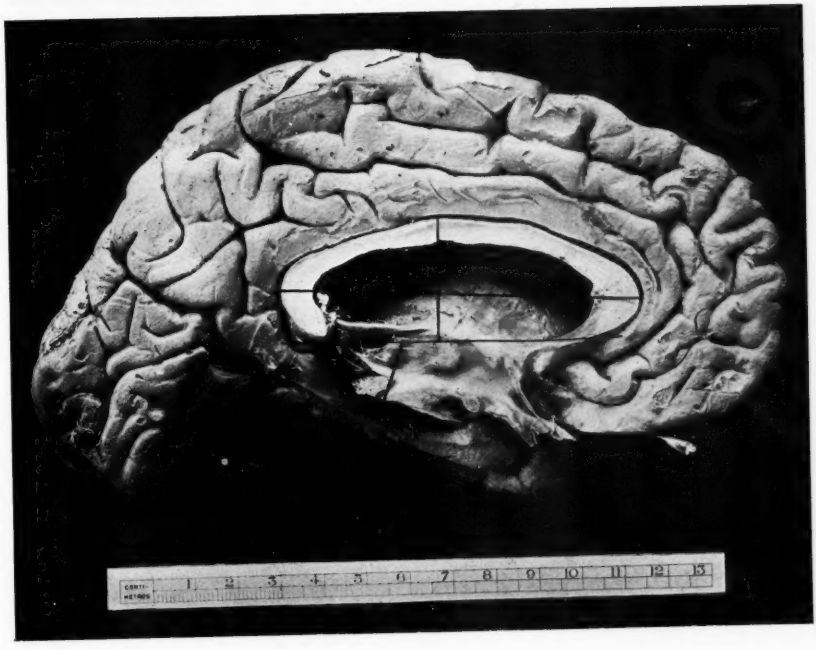
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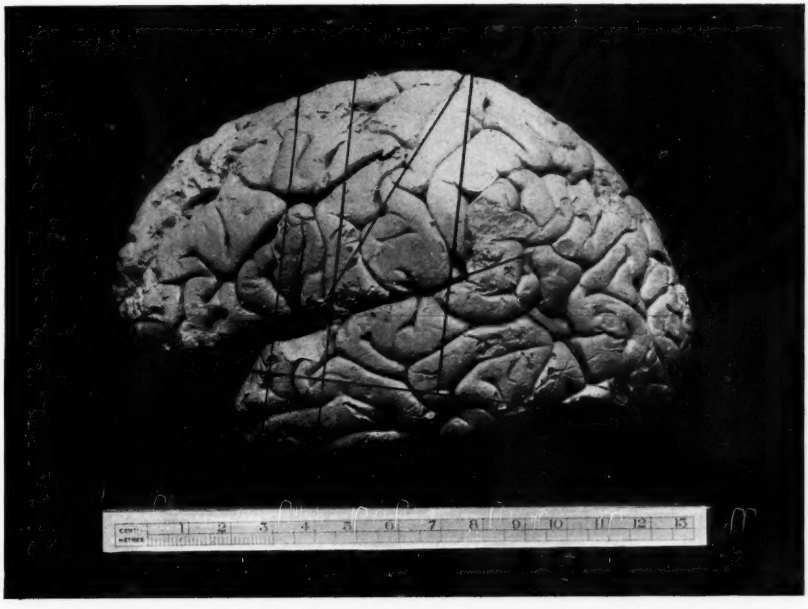
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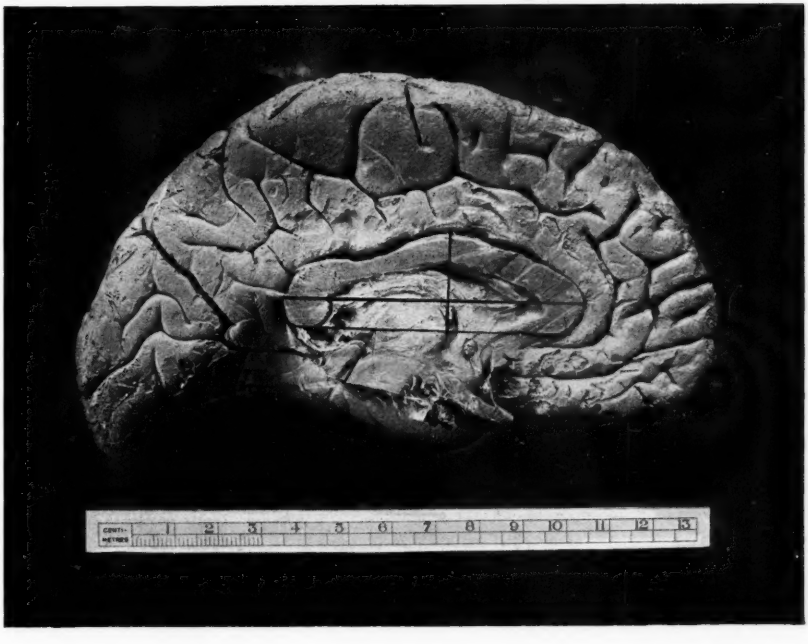
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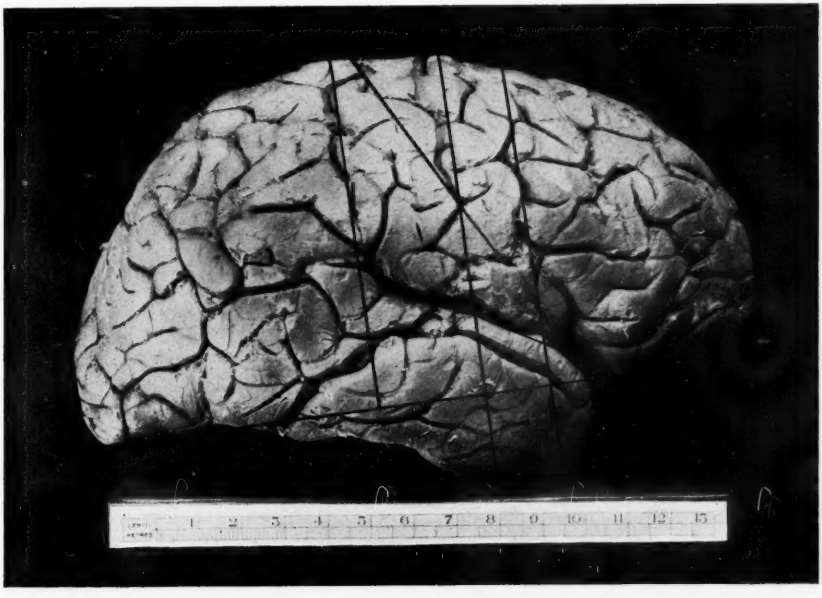

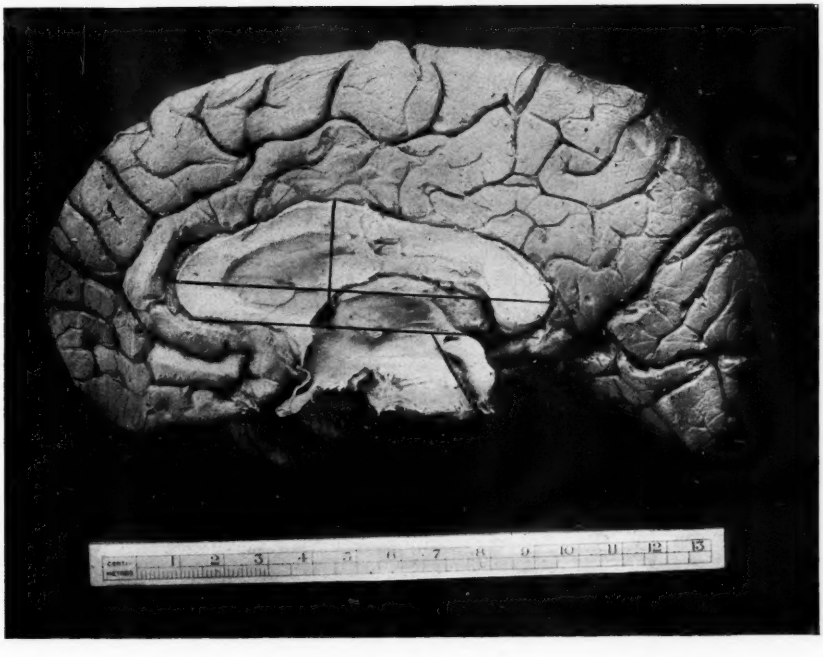

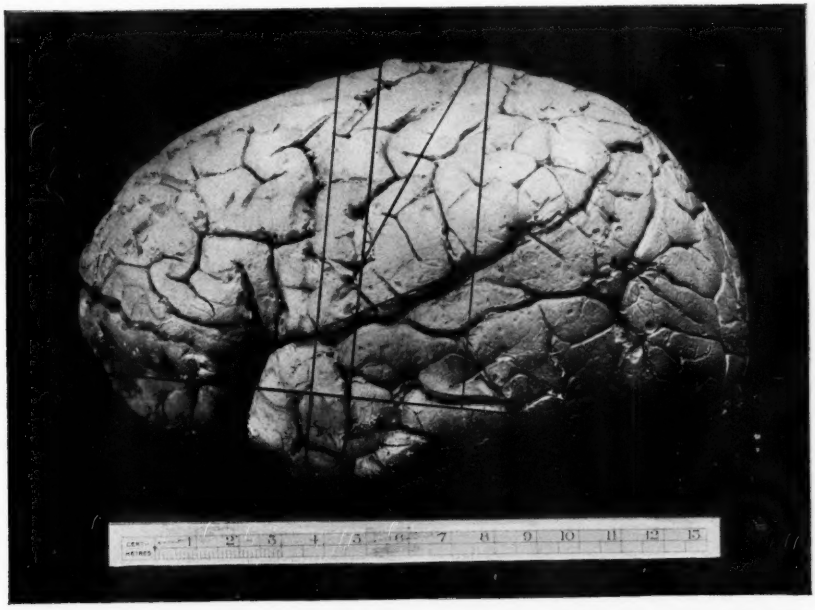

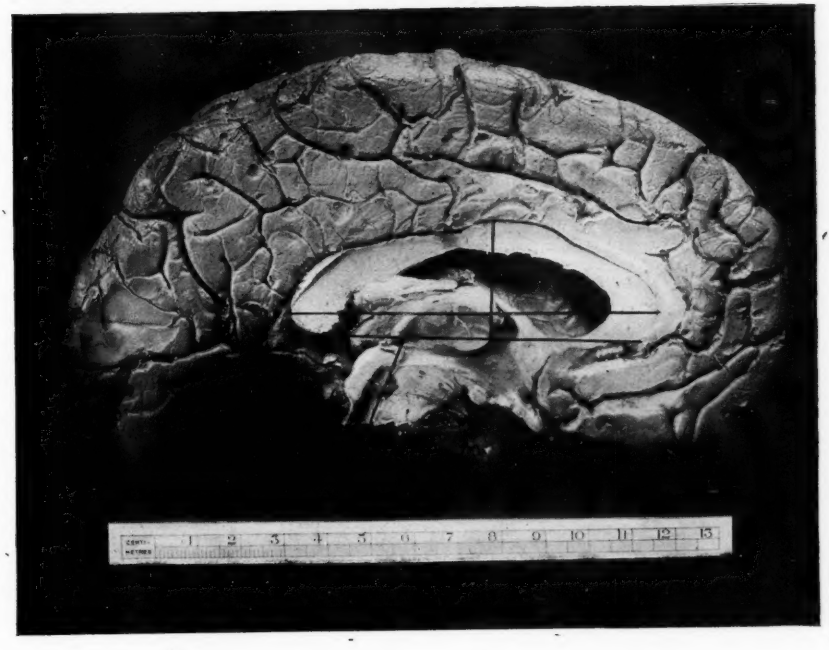

ON THE CAVUM SEPTI PELLUCIDI

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I. INTRODUCTION

In the course of a recent interesting and stimulating discussion Prof. R. A. Dart (1) has penned the following passage:

"No closer parallel between the evidence of development and comparative anatomy could be found than that afforded by the history of the septum pellucidum. It has been stated that the septum or lamina terminalis is solid during the first three months of human foetal life. This is a foetal condition of affairs repeated by all Mammalia during their embryonic history, whether they possess a corpus callosum or not, but with this difference: the condition of a solid septum is found in man only during early foetal life, while it is permanent throughout life in Monotremata (Prototheria), in Marsupialia (Metatheria) and in many of the Eutheria—e.g. Edentata, Rodentia, Carnivora and Cheiroptera. Thus Piersol (1919) states that 'The septum lucidum of man is the rudimentary representation of what in many of the lower (macrosmatic) animals is a much more important tract of cortical substance. In some animals, as for example, the rabbit, cat and dog, the septum is solid, a cleft never appearing in it.' So far as I know the actual range of the occurrence, amongst Eutheria, of a cleft in the septum has not been fully investigated.... In view of these facts already ascertained, there need be no question of a closure of the ventricle, since it has been enclosed from the beginning wherever it has occurred amongst Mammalia."

A study of the context from which the above quotation is taken shows that, if I understand him aright, Prof. Dart maintains the following theses: (*a*) The cavum septi pellucidi is absent in the animals above indicated; (*b*) In all those animals in which a cavum is present it is *closed*, i.e. completely sur-

rounded by brain tissue and not in communication with any other brain cavity nor with the exterior of the brain (intercerebral fissure); (*c*) In all early mammalian embryos, including that of Man, the septum pellucidum is solid, and in those cases (such as Man) in which a cavum appears it is developed as a cleft in the previously solid septum, never communicating with the outside and not being derived from the intercerebral fissure.

II. COMPARATIVE ANATOMY

Bearing in mind Prof. Dart's statement concerning our need of a survey of the occurrence of the cavum septi pellucidi, I have made some notes upon this point during the course of certain reading which I have recently had occasion to do. The results are now presented, together with certain personal observations, in the hope that they may be of some use to investigators along this line, as well as by reason of the fact that when they are considered in conjunction with certain of the statements and views of Prof. Dart some interesting points arise for discussion. I make no pretence, however, of having carried out a complete survey of the literature or of the class Mammalia.

For our present purpose there are two facts which we wish to know concerning the cavum in any given animal: (*a*) Is it present or absent? (*b*) If present, is it closed or open—i.e. in communication with the intercerebral fissure?

Monotremata and Marsupialia

So far as I am aware, a cavum septi pellucidi has never been described in any of these forms.

Edentata

In the sloths (Bradypodidae) Elliot Smith (55) describes a narrow cavum opening downwards and forwards.

Forbes (20) states that in *Myrmecophaga jubata* there is a fifth ventricle; from his figure of a median section of the brain and from a similar figure of Elliot Smith's (55) I *infer* that the cavum is open antero-inferiorly in the interval depicted between the genu of the corpus callosum and the anterior commissure and fornix[1].

[1] Of the liability to error which is inherent in such an inference I am well aware. It is difficult to imagine a better illustration of this danger than that afforded by Plate XXXIII illustrating Tiedemann's paper "On the Brain of the Negro, compared with that of the European and the Orang-Outang," in *Phil. Trans. Roy. Soc. Lond.* vol. CXXVI, 1836, p. 497. This plate depicts the brain of a male negro in which the corpus callosum is shown without a trace of a rostrum, and therefore with its genu widely separated from the anterior commissure and the fornix, the interval being occupied by the septum pellucidum. From this one would have inferred that the cavum septi pellucidi was open. Yet practically to a certainty that was not the case, for Tiedemann insists that "in the internal structure of the brain of the negro I did not observe any difference between it and that of the European," and in this connection he mentions specifically the corpus callosum, fornix, commissures and *septum lucidum*. With such an instance in my mind, the reserve with which I draw this inference from the figures of Forbes and of Elliot Smith needs no further protesting. I have ignored all such inferences in framing my theoretical conclusions, which are based solely upon well-attested observations.

According to Elliot Smith, in the armadillos (Dasypodidae) there is practically no septal part of the paracommissural body; hence, presumably, there is no cavum.

The same investigator states that in the pangolins (Manidae) "the condition most nearly approaches that of the sloths."

Neither Elliot Smith (55) nor Woollard (73) describes a cavum in *Orycteropus*, but the latter author illustrates it in his fig. 60; it is likewise depicted, but not labelled, in his figs. 57 and 59. From his illustrations (figs. 47 and 63) of the medial aspect of the brain, in which the genu of the corpus callosum appears widely separated from the ventral and hippocampal commissures, one would infer that the cavum is open antero-inferiorly, and his figs. 57, 59 and 60 show clearly that this is indeed so, the inference in this case being shown to be correct.

Ungulata

Artiodactyla. Flower (18), Honegger (28) and Fiske (17) describe a cavum in the *sheep*, whilst Burkholder (10) refers to its *occasional* occurrence. None of these authors indicates clearly whether it is open or closed, but the photographs constituting Jakob and Onelli's (31) fig. 212 and Fiske's fig. 9 indicate closure; they may be compared with Burkholder's Plate VIII, O'Donoghue's (44) fig. 119, Wilckens' (69) fig. 72, and fig. 1 illustrating this paper. According to Déjerine (15), Verga's ventricle—see (62)—is large in the sheep.

Mingazzini (40) states that, according to Tenchini, *Bos taurus* possesses a cavum which (like the septum) reaches to the hinder end of the corpus callosum; Honegger (28) likewise finds a cavum in the calf. Neither author indicates whether it is open or closed; Bütschli's figures (11) suggest the latter, as does Montané and Bourdelle's (42) fig. 107.

Honegger expressly denies the existence of a cavum in the *pig*.

Brandt (4) describes and figures a cavum in *Auchenia lama*, but does not indicate whether it is open or closed.

Perissodactyla. Mingazzini cites Tenchini as authority for the statement that in the Perissodactyla (Einhufern) there is a cavum which extends to the splenium of the corpus callosum.

Sisson (51) and Bradley (3) describe the septum in the *horse* as consisting of two laminae in contact with each other; according to Franck (21) the horse, like Man, possesses a closed cavum. Honegger (28) and Montané and Bourdelle (42) likewise ascribe to the horse a cavum, though this animal does not appear in the list of material examined by Honegger; according to Percivall (47): "Sometimes this fissure is very demonstrable, glistening interiorly with moisture; at other times it is hardly perceptible." Franck's opinion that the cavum is closed is supported by Martin's (39) fig. 165 (which depicts a median section of the brain of an advanced horse embryo), likewise by Montané and Bourdelle's fig. 112 and Bradley's (3) fig. 86. Déjerine (15) states that Verga's ventricle is large in the horse.

Rodentia

Since considerable theoretical importance has been attached to the statement in Piersol's *Human Anatomy* that in the rabbit, cat and dog the septum is solid, a cleft never appearing in it, I have endeavoured to ascertain beyond doubt the state of affairs in these animals.

In addition to the mention of a cavum septi pellucidi in the *rabbit* in many standard manuals of practical zoology and in the work of W. Krause (34), we have the following authoritative account of the cavum in this animal from Prof. Elliot Smith (52): "In the rabbit, however, one may already see evident signs of the tendency of the growing corpus callosum to extend beyond the rudimentary septum. Thus, while the grey mass still fills up the greater part of the angle between corpus callosum and fornix commissure, the anterior extremity of the former is growing forwards and stretching the part of the lamina in which it lies. There is thus produced (fig. 13, *c.s.*) a depression *widely open in front* and roofed above by the anterior extremity of the corpus callosum. The lateral walls of this depression are formed partly by a stretching of the thickening of the lamina terminalis, and possibly in part by the pre-commissural area" (italics mine).

I have carefully examined a number of rabbits' brains in the manner described below in the account of the cavum in the cat, and I have never failed to observe a small but indubitable cavum, freely open (into the inter-cerebral fissure) antero-inferiorly, exactly as described by Elliot Smith.

Honegger (28) denies the existence of a cavum in the rabbit and *mouse*.

Carnivora

Ziehen (75) states that in this group the cavum is generally absent; according to Elliot Smith (52) it is either small or absent.

As already mentioned, in Piersol's *Human Anatomy* the *cat* is included in a short list of animals in which the cavum is stated to be absent; Honegger (28) finds likewise, whilst according to Franck (21) not only does this animal lack a cavum but even the septum is almost absent. Martin (38) seems to describe an incipient caval development in cat embryos which is later obliterated with the production of a solid septum; Elliot Smith (54) also places this interpretation upon Martin's work. On the other hand, the existence of a cavum in this animal is mentioned by Mivart (41), Wilder and Gage (70), Reighard and Jennings (48) and Winkler and Potter (71).

I have examined a number of brains of rabbits, cats and dogs (i.e. the animals named in Piersol), for which material I have to thank Prof. John Tait and Dr H. E. Burke of the Department of Physiology and Experimental Medicine and Prof. R. L. Stehle of the Department of Pharmacology of McGill University. I have chosen to base the account of my investigations upon the work done on the cats' brains because this material yielded my best specimens

and has therefore been selected for the purpose of illustrating this communication (figs. 1 and 2).

The animals, which had been utilised for experimental work in the departments mentioned, were decapitated, the scalp and the vault of the skull were removed and the dura mater was freely incised. The heads were then immersed in formalin for some days, after which the brains were removed and examined, the specimens being preserved in alcohol. Although my best specimens were obtained from formalin-hardened material, all the observations were carefully confirmed by the examination of perfectly fresh brains. The brains of the three species mentioned were investigated in the same manner.

The specimens obtained by sectioning the brains as accurately as possible in the median plane were rejected as affording no evidence upon which reliance could be placed, by reason of the extreme narrowness of the cavum in the animals in question.

Instructive preparations of the brains of all three species were obtained by the following simple method. The brain was split by a paramedian section a few millimetres from the median plane, say on the right side. Most of the right frontal pole was then amputated by a coronal section a few millimetres anterior to the genu of the corpus callosum, the latter being readily identified by slightly separating the two frontal poles. What remained of the right frontal pole was now gently drawn away from the medial aspect of the left cerebral hemisphere from the corpus callosum downwards towards the base of the brain and the leptomeninges were removed from this region, the utmost care being exercised throughout not to inflict the slightest injury of any kind upon the nervous tissue. This was done partly under a dissecting microscope which permits of a dissection of this kind being completed without taking one's eye off it (61).

In the specimens thus prepared it is very easy to demonstrate a small recess or diverticulum of the intercerebral fissure extending backwards and upwards in the median plane beneath the anterior extremity of the corpus callosum. This cavity is so small and, particularly in the rabbit, it extends backwards for so short a distance that it is easy to understand how it might be overlooked entirely, or, if noticed, regarded simply as a portion of the intercerebral fissure. Unfortunately such specimens do not lend themselves very well to representation for purposes of illustration, but they serve as valuable guides in the preparation of another series of specimens, namely coronal sections, inasmuch as they reveal exactly where to make such sections so that they will pass through the recess in question.

Coronal sections through brains of rabbits, cats and dogs were made, using the above-described specimens as guides, and they proved most instructive. Fig. 2 is a photograph of such a section of the brain of an adult cat, made at the level indicated by the vertical line in fig. 1. One recognises the corpus callosum and beneath it, within the substance of the cerebral hemispheres, the lateral ventricles, each of which appears as a curved slit. Clearly the structure

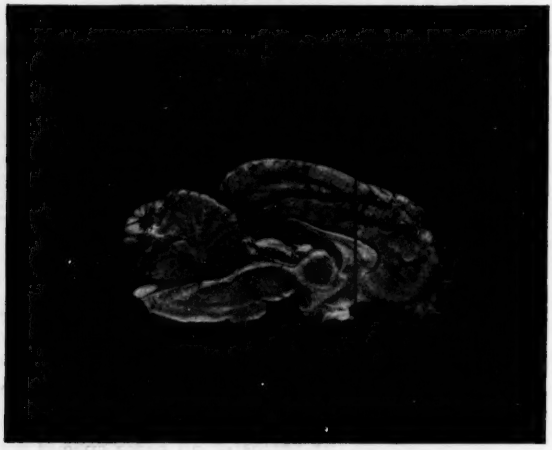

Fig. 1. Photograph of median section of brain of adult cat. The vertical line indicates the level of the coronal section depicted in fig. 2.

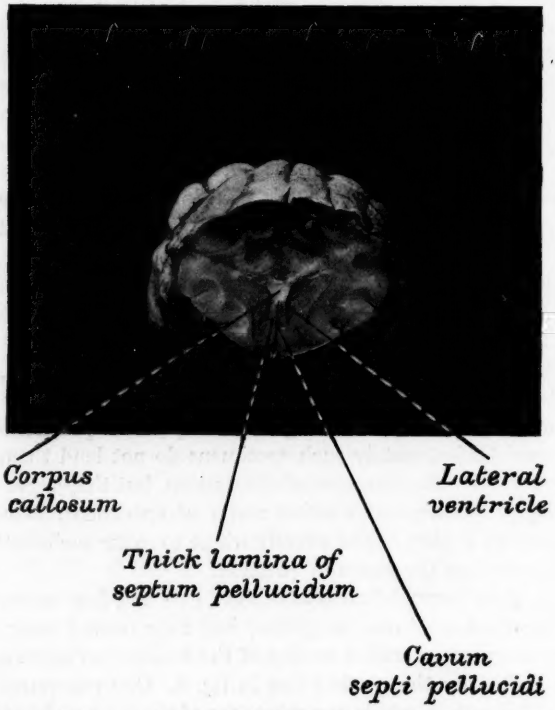

Fig. 2. Photograph of coronal section of brain of adult cat. Posterior segment of brain, viewed from the front.

forming the medial wall of the lateral ventricles is the septum pellucidum, which is relatively thicker in these macrosmatic mammals than in microsmatic man; I cannot agree with Reighard and Jennings that it is translucent in the cat. It is obvious that this septum is bilaminar, its right and left halves being separated by a very narrow, slit-like cavity which extends downwards to the base of the brain, where it is bridged over by a thickening of the leptomeninges containing blood vessels. It might be argued that the lower part of this slit is merely a portion of the intercerebral fissure, but this certainly cannot apply to the upper part of the slit which is *actually interposed between the lateral ventricles.* This narrow cavity, existing within the substance of the septum pellucidum, can be none other than the cavum septi pellucidi. It is known from a comparison with the other specimens that this cavity is identical with the recess mentioned above, hence clearly not only is a cavum present but it is open antero-inferiorly. It is very small, however, and this is particularly the case in the rabbit; I should think that without the guidance of such specimens as those described above one would be much more likely to miss the cavum than to strike it in coronal sections.

In respect of the conformation of the corpus callosum and septal region my fig. 1 agrees closely with Reighard and Jennings' (48) fig. 143 and the first figure on the plate facing the second page of the introduction to Winkler and Potter's *Anatomical Guide to Experimental Researches on the Cat's Brain* (71). On the other hand, as regards the anatomy of the front end of the corpus callosum, my fig. 1 differs from Mivart's (41) fig. 129, Wood Jones' (33) fig. 17 and Martin's (38) fig. 4; one must remember, however, that the latter represents the brain of a 9 mm. kitten. In this connection Martin writes: "Dadurch endlich, dass sich der umgebogene Nasalteil des Balkenquerschnittes durch Zulagerung neuer Fasern aus dem Frontalteile der Hemisphäre verlängert, nähert er sich wieder der Lamina terminalis (fig. 4) und schliesst endlich den Bogen ganz ab, so dass das ursprünglich ventral noch freie Septum pellucidum nun ganz vom Balken umringt ist." No cat's septum pellucidum studied by me (I have examined adults only) was either completely solid or entirely surrounded by corpus callosum, as maintained by Martin.

My fig. 2 resembles Reighard and Jennings' fig. 149 except that, representing (as my fig. 1 indicates) a section made behind the genu of the corpus callosum, it shows a more extensive cavum than does their figure, which depicts a section through the genu. Somewhat curiously, Winkler and Potter do not show the cavum (at any rate not distinctly) in their Plate IV—doubtless because they were not interested in it.

In his figure of a median section of the brain of a *lion*, Tiedemann (63) refers to what is clearly septum pellucidum as "Lamina dextra septi medullaris," thereby indicating the existence of two laminae, right and left, and hence of a cavum. The figure is not sufficiently clear in this region to justify a positive opinion, but in view of the condition obtaining in the cat it may be provisionally assumed that the cavum is open in the lion also.

Although its existence is denied by Honegger (28), a fifth ventricle in the *dog* is mentioned in such authoritative works as Ellenberger and Baum's *Anatomie des Hundes* and Charnock Bradley's *Dissection of the Dog*, also by Howell (29); none of these, however, indicates whether it is open or closed. Since I have invariably demonstrated the presence of an open cavum in this animal by the methods described above, the statement that the septum is solid in the rabbit, cat and dog is shown to be incorrect.

Pansch's (46) figure (Taf. 14, fig. 2) of a median section of the brain of a *fox* and Brühl's of fox (7) and *wolf* (8) indicate the presence of open cava in these species, as one would expect.

Johnston (32) has published figures of transverse sections of the brain of the *bear* (his figs. 73–75) which, upon comparison with my fig. 2, appear to constitute evidence of the presence of an open cavum in this animal, a conclusion strengthened by Brühl's figures of median sections (9).

Insectivora

According to Ganser (22) the *mole* (*Talpa europaea*) lacks a cavum.

Primates

For information concerning this important group I turned with high hopes to Gustaf Retzius' monograph, *Das Affenhirn* (50). He was not concerned with the septum and cavum, however, and makes no mention thereof in his text; the majority of his illustrations, magnificent though they be, do not reveal the conditions in this region of the brain sufficiently clearly to warrant drawing inferences from them. Regretfully, therefore, with one or two exceptions referred to below, I have felt constrained to pass over the wealth of material represented in this great monograph.

Van der Kolk (64) depicts a median section of the brain of *Stenops kukang* (*Nycticebus javanicus*); clearly he applies the two names to the same animal. For reasons which will appear presently it is of some interest to endeavour to ascertain precisely which animal this is. Neither Forbes (19) nor Elliot (16) mentions *Stenops kukang*, but Forbes gives *Nycticebus javanicus* and *S. javanicus* as synonyms of *N. tardigradus*, whilst Elliot gives *N. tardigradus*, *S. tardigradus* and *Tardigradus coucang* as synonyms of *Nycticebus coucang* Boddaert; he likewise gives *Stenops javanicus* as a synonym of *Nycticebus javanicus* E. Geoffroy. My conclusion is that van der Kolk studied a specimen of the latter species; his figure will be discussed in connection with the following.

Vrolik (67) gives a brief description and some figures (including a median section) of the brain of *Loris paresseux*, which from van der Kolk's paper (p. 283) I learn to be *Lemur* (*Stenops*) *tardigradus*. These figures are reproduced (with added clearness) in (68), where the animal is referred to definitely as *Stenops tardigradus*; this I gather to be either the *Loris gracilis* referred to by

Forbes (and this, in turn, might be either the *L. tardigradus* Linnaeus or the *L. lydekkerianus* Cabrera recognised by Elliot) or else (and, I think, more probably) it is the *Nycticebus tardigradus* mentioned by Forbes (i.e. the *N. coucang* Boddaert recognised by Elliot).

In short, van der Kolk and Vrolik examined the brains of two closely related species. It has seemed desirable thus to establish this because their figures differ very remarkably. Vrolik (67) mentions the septum lucidum in his text, but not the cavum; his figure suggests clearly an open cavum. Van der Kolk's figure (Plate V, fig. 3) shows a condition of the corpus callosum and septal region which suggests to my mind the possibility of his having fortuitously encountered a brain with an anomalous corpus callosum and septal region; such cases are well known in Man—see (62) and certain of the references therein given—and they have also been observed in other Mammals, e.g. the cat. His text does not elucidate the matter, so far as I can make out. Another complexion is put upon it, however, by a passage in Vrolik's publication of which the following quotation will serve to indicate the tenor: "...La description anatomique, que Van der Kolk donne de l'animal, s'éloigne tellement de nos connaissances sur la structure des Mammifères, que si elle était juste, le *Loris de Java* deviendrait presque un être anormal....Je pense que Monsieur van der Kolk aura été induit en erreur, et par l'état peu favorable dans lequel se trouvait l'individu qu'il avait à sa disposition...," etc. With these possibilities, error and anomaly, thus before us, we must perforce ignore van der Kolk's figure; Vrolik's, however, carries its measure of conviction, at least to my mind.

In *Tarsius* Elliot Smith (56) describes a cavum freely open below between the corpus callosum and the psalterium.

Retzius' figures (50) suggest an open cavum in *Hapale*.

His Taf. V, fig. 14, in the same monograph speaks for a closed cavum in *Ateles*, a condition suggested likewise by one of Huxley's figures (30).

Leuret's figure of the brain of a *baboon*, reproduced by Vrolik (68), suggests a closed cavum in that animal, as does Vogt and Specht's illustration (65).

In *Simia nemestrina*, which I learn from Elliot (16) is the pigtailed macaque, *Pithecus nemestrinus* (Linnaeus)—commonly referred to as *Macacus nemestrinus*—Tiedemann (63) mentions the "Septum cerebri lucidum, ex duabus trigonis medullae laminis constans," thereby indubitably indicating the presence of a cavum. His figure (Tab. I, fig. 7) suggests that the cavity is closed; this figure presents certain features, however (these need not occupy space here), which incline me to lighten somewhat the weight which might be attached to it.

Through the kindness of Prof. F. D. Geist of the Department of Anatomy of the University of Wisconsin, who gave me a beautifully formalin-fixed brain of *Macacus rhesus*, and of Profs. Herbert M. Evans and Miriam E. Simpson of the Department of Anatomy of the University of California, who enabled me to procure a fresh brain of this species, I have been enabled to examine the brain of this monkey by precisely the same methods as in the

case of the rabbit, cat and dog, and with a like result, namely, the demonstration of the existence of a small but indubitable open cavum.

Vrolik's (68), Gegenbaur's (23), and Jakob and Onelli's (31) figures of the brain of the *orang-outang* bespeak a closed cavum; likewise Retzius' illustrations (50), on the whole, although they do not all look quite alike.

Müller (43) describes and figures the cavum in the *chimpanzee*. His description indicates that the cavum is closed antero-inferiorly, a point upon which Brühl's (6) and especially Symington's (60) beautifully clear figures leave no doubt. It is of some interest to note that Owen (45) reproduces a figure of van der Kolk and Vrolik's which in this respect presents an appearance identical with Tiedemann's figure of the negro brain (reproduced by Owen on the same plate); one feels justified in assuming that both these figures are inaccurate in respect of this feature. It is a curious fact that elsewhere, however, Vrolik (66) has a figure more in agreement with those of Brühl and of Symington. Retzius' (50) figures suggest a closed cavum, but it is fortunate that we are not dependent upon them for our knowledge of the cavum in this animal. Young's (74) fig. 25, a photograph of a median section of the brain of a chimpanzee, has a leader bearing the caption "Aditus ad ventr. s. pell." and leading to an indistinct mark in the region of the rostrum of the corpus callosum; in the absence of enlightenment in the text one is left wondering at this mystery, which is deepened by being repeated in his fig. 27, a photograph of a median section of "the brain of an old man in which the septum pellucidum is considerably extended vertically on account of hydrops ventriculi."

In his work on the brain of the *gorilla* Bolk (2) does not mention the cavum. Unfortunately many of his figures are very sketchy, especially in the region of the septum (with which his investigation was not concerned); however, his figs. 26–29 clearly suggest the presence of a cavum, whilst his fig. 18 and Elliot Smith's (58) figs. 247 and 248 all definitely depict an absolutely humanoid degree of development of the genu and rostrum of the corpus callosum, thereby indicating that the cavity is closed. Elliot Smith (58) describes and figures a large ventricle of Verga in the brain of a gorilla (referred to as *Anthropopithecus gorilla*) preserved in the Museum of the Royal College of Surgeons of England; he mentions the absence of this cavity in another specimen.

It is common knowledge that in *Man* a cavum is present and is completely closed. In his *Human Embryology* Minot quotes B. G. Wilder as stating *in litteris* "that in man and anthropoids it is wholly circumscribed by brain tissue."

Mammalia in general

After describing the fifth ventricle freely open below between the corpus callosum and the psalterium in *Tarsius*, Elliot Smith (56) states that "in spite of a very generally expressed belief to the contrary, this is the condition which

prevails in the vast majority (practically in all) of the Eutheria." This from so eminent an authority and based, as he points out at the beginning of the communication in question, upon the examination of what is probably an unprecedented collection of representative mammalian brains, together with the facts set forth above, seems to constitute a warning against the unreserved acceptance of the generalisations that the septum pellucidum is solid in the Edentata, Rodentia and Carnivora and that the fifth ventricle is closed wherever it occurs amongst Mammals. Similar statements are not rare in the literature, but further quotation and criticism would be profitless.

From the foregoing it would appear that Mammals may be classified somewhat as follows upon the basis of the presence and condition of the cavum septi pellucidi:

Mammalia
- *A.* Cavum absent (septum solid) — e.g. Marsupialia, mole
- *B.* Cavum present (septum bilaminar)
  - (*a*) Cavum open, e.g. cat, *Tarsius, Macacus*
  - (*b*) Cavum closed, e.g. chimpanzee, man

III. ONTOGENY OF THE OPEN CAVUM

Under this heading I cannot do better than quote the following account from the pen of Prof. Elliot Smith (52).

"In the higher or microsmatic Mammal, a time soon arrives when the growing commissural arc reaches the limits of the small thickening of the lamina terminalis. In tracing the development, the lamina appears therefore to atrophy, but this apparent atrophy is largely, if not wholly, relative. The lamina becomes moulded to the shape of the commissure by the growth of the latter, so that at an early stage in the developing microsmatic Mammal, the dorsal commissure consists of an arc of fibres, with a thin layer of grey matter inclosing them, and accurately adapted to the shape of the commissural arc. There is thus early produced a small recess roofed by corpus callosum (lying in the lamina terminalis), bounded posteriorly and below by the fornix commissure (also inclosed in the lamina terminalis), and laterally by walls also formed from the stretched lamina terminalis. This small recess, which is freely open in front, so as to communicate with the great longitudinal fissure, is the rudiment of the 'cavum septi pellucidi.' As the commissure increases in extent by the addition of new fibres, the stretching of the lamina terminalis still goes on, so that as the corpus callosum grows back the cavum increases in extent, and the 'laminae septi pellucidi' become broader and longer."

From this it is clear that the open cavum is developed as a diverticulum or recess from the intercerebral fissure which invades a previously solid septum. To my understanding, at any rate, such an origin of the cavum does not imply that it is a portion of the fissure partially shut off by a process of concrescence of the two cerebral hemispheres to form the septum, as has been thought. The

principal factor in the formation of the cavum appears to be the growth of the corpus callosum; with Dart we may add to this the lateral pull of the lateral elements of the fornix—see (62).

This authoritative account of the development of the open cavum as a recess communicating with the intercerebral fissure must be taken as subjecting to modification the statement that the cavum "has been enclosed from the beginning wherever it has occurred amongst Mammalia."

IV. PHYLOGENY OF THE OPEN CAVUM

Judging from the conditions obtaining in the brains of Monotremes (53) and Marsupials (18), the evolution of the cavum within a previously solid septum would appear self-evident.

The comparative anatomical facts set forth in section II suggest that the cavum septi pellucidi made its phylogenetic *début* in a primitive eutherian brain most nearly represented in our extant fauna by that of certain of the Edentates. Furthermore, the fact that in the Edentates and, as far as I am aware, in all sub-primate Mammals which possess it (save, doubtfully, certain Ungulates), the cavum is in communication with the intercerebral fissure below the genu of the corpus callosum, together with the mode of development of this type of cavum, constitutes strong evidence in favour of the view that it was evolved as a recess or diverticulum of the intercerebral fissure, in open communication therewith.

Concerning the phylogenetic factors which have operated to produce such a cavum Elliot Smith (52) writes: "...In the mammalian series, as the corpus callosum is rapidly increasing in extent, the 'commissure-bed' is diminishing in extent with the lessening importance of the olfactory sense. These two opposing factors have very important effects upon the morphology of this region in the higher Mammals. The stretching of the thickened mass of the lamina terminalis by the extending arc of the dorsal commissure produces the septum pellucidum; and as a physical expression of the antagonism between the extension of the commissure and the retrogression of its 'matrix' the cavum septi pellucidi or fifth ventricle appears." He has also described this phylogeny in another publication (54), where it is illustrated by a series of excellent schemata. Following Dart, we may add to these factors the phylogenetic attenuation of the hippocampal commissure, which allows the lateral pull of the lateral elements of the fornix to be exerted upon the septum pellucidum during ontogeny.

V. ONTOGENY OF THE CLOSED CAVUM

Unless otherwise stated, my remarks under this heading are to be understood to refer to Man, for, so far as I am aware, this seems to be the only species in which embryological observations upon this type of cavum have been made.

Prof. Dart has reviewed some of the work which has been done upon this subject and has discussed the two divergent views which have been put forward. According to one view the cavum septi pellucidi is a portion of the intercerebral fissure which has been shut off, as it were, by the concrescence of the cerebral hemispheres and the development of the various commissures, the septum pellucidum thus being cortical in origin and bilaminar *ab initio*. According to the other view the septum pellucidum is derived from the lamina terminalis and the cavum is developed as a cleft appearing within the previously solid septum as the result of the operation of certain mechanical strains to which it is subjected by the developing commissures and fornix. Prof. Dart mentions that his library facilities were limited, and without doubt this fact is responsible for certain historical inaccuracies implied, rather than stated, in his discussion; I am venturing to attempt to correct these lest they become perpetuated in the literature.

Dart writes: "The ontogenetic history of the human septum pellucidum has been investigated by Marchand (1891, 1909), by Zuckerkandl (1901) and by Goldstein (1903). As Streeter (1912) has pointed out, Zuckerkandl (1901) believed that during the formation of the commissures, 'There is an approximation and fusion of a considerable area of the median walls (of the hemispheres) with resorption of the previously interposed mesodermal falx. This forms a "massa commissuralis" through which the fibres subsequently cross.' With this view, however, the other embryologists are in sharp disagreement, for Marchand failed to find any concrescence of the cerebral hemisphere walls but showed instead that until the fourth month of foetal life the septum pellucidum is a single solid homogeneous cellular mass interposed between the two lateral ventricles, but that during the fourth month a cavity appears within the previously solid mass; this cavity enlarges as the septum grows and becomes the ventricle of the septum—the septum now becoming bilaminar for the first time." Again, referring to the homology of the human septum pellucidum with the lamina terminalis: "If Zuckerkandl's description of commissural development in Man were correct, this homology would be untenable."

Evidently Dart is under the impression that Zuckerkandl studied the development of the septum in the *human* embryo: presumably he gained that impression from the above-quoted passage in Streeter's account of the development of the central nervous system in Keibel and Mall's *Manual of Human Embryology*. Perusal of Zuckerkandl's paper (76), however, reveals that he worked with *rat* embryos; it would seem to be Prof. Streeter's omission to mention this fact in a manual of *human* embryology which caused Prof. Dart to presume (quite justifiably) that Zuckerkandl had studied the development in Man. Similarly, Johnston (32) writes: "Mihalkovics, His and Zuckerkandl have held that the corpus callosum forms in a secondary area of fusion of the medial walls of the hemispheres," but he omits to mention that Mihalkovics studied the development in the rabbit, His in Man and Zuckerkandl in the rat!

Well might Goldstein exclaim (26): "Die Entwickelungsvorgänge können bei verschiedenen Tieren ganz verschieden verlaufen."

Prof. Dart is likewise under a misapprehension when he writes: "Marchand failed to find any concrescence of the cerebral hemisphere walls," etc. Marchand (36) describes such concrescence very definitely, and he describes the cavum septi pellucidi as developing within the area of this concrescence; it was Goldstein (25) who denied its occurrence, which, however, has recently been upheld by Broman (5). Certain authors, e.g. Goldstein (24), Ziehen (75) and Johnston (32), correctly attribute to Marchand the view that concrescence of a portion of the hemisphere walls occurs, within which area the cavum septi pellucidi arises by a secondary splitting or cleavage. They all fail to point out, however, that whilst Marchand describes the concrescence and the *situation* in which the cavum arises as matters of observation—i.e. of *fact*—he is very careful indeed to state the *manner* of its origin (by a process of interstitial cleavage) as a matter of *opinion* only, for he did not observe the very beginning of the cavum. He supports this opinion by referring to animals lacking a cavum: in this Dart follows him; I have shown above, however, that some of the statements which have been made concerning the comparative anatomy of the cavum are not above reproach. Langelaan (35) comes to a conclusion apparently practically identical with the opinion held by Marchand.

In a later publication (37) Marchand, referring to a foetal brain of the fifth month, states that an inferior boundary to the septum pellucidum is not recognisable; the brain in question is depicted in fig. 16 of his earlier paper (36). Again on p. 398 of his later work (37), in a schema illustrating three stages in the development and growth of the corpus callosum, he denotes the rostrum by a dotted line in the first two stages and by a continuous line in the last stage only, thereby suggesting that in the first two stages the rostrum is undeveloped, leaving the septum open below. It will be realised that although, if the septum be "open" below, between the genu of the corpus callosum and the anterior commissure (the rostrum being absent or rudimentary), the probability is that the cavum is open in like fashion, nevertheless it is quite possible for the cavum to be closed though the septum be "open"—cf. footnote on p. 60 and the illustration therein mentioned. Goldstein's statement that the *cavum* is open in his embryo of the fourth month is, however, quite positive; equally so is Kollmann's assertion that the cavum is open downwards at first, the opening being later closed by the rostrum of the corpus callosum. Some of Retzius' beautiful figures (49), e.g. his Taf. 4, fig. 10, which depicts the brain of an embryo of the fourth month measuring 15 cm., seem to show very clearly an open cavum, which appears closed in the figures of later stages. In a human embryo of the second half of the fourth month, measuring 10·5 cm. (crown–rump), Goldstein (25) describes the cavum as being definitely open, and maintains that it is a portion of the intercerebral fissure shut off not by a fusion of the cerebral hemispheres (the occurrence of which phenomenon he denies), but by the development and growth of the rostrum

of the corpus callosum. His figs. 2, 4 and 5 (Taf. IV) show the *septum* freely open downwards between the genu of the corpus callosum and the anterior commissure. His youngest specimen appears to have been about the same stage as Marchand's youngest, but whereas Marchand was not certain as to the condition of the *cavum* (whether open or closed), Goldstein expresses no doubt upon the point.

Hochstetter (27), however, feels certain that such open cava are artefacts and gives a convincing account of the development of the cavity by interstitial cleavage.

It may be provisionally concluded that the best evidence at present available favours the view that the cavum arises by interstitial cleavage in the lamina terminalis, before the development of the genu and rostrum of the corpus callosum, the latter subsequently preventing any communication between the cavum and the intercerebral fissure.

Prof. Dart has rendered valuable service by directing our attention to the probable rôle in the genesis of the cavum played by the laterally directed component of the oblique pull of the lateral elements of the fornix.

VI. PHYLOGENY OF THE CLOSED CAVUM

Prof. Dart suggests that the phylogenetic attenuation of the hippocampal commissure has been the essential factor in the evolution of the cavum, this attenuation permitting the septum to be rent into two lamellae during ontogeny by the lateral component of the oblique pull of the lateral elements of the fornix. This view receives support from the fact that in forms with a stout hippocampal commissure, as the Marsupials, that structure is sufficiently strong to resist the lateral pull referred to, hence no cavum is developed. But Dart does not admit the occurrence amongst Mammals of an open cavum; it therefore receives no recognition in his scheme of phylogeny. In view of the observations set forth above, however, it would appear that the question of the phylogeny of the closed type of cavum, as exemplified in Man, is yet open for discussion in which cognisance shall be taken of the occurrence of the open cavum.

Although we have excellent accounts of the brains of certain Menotyphla (*Macroscelides*, *Ptilocerus*, *Tupaia* and *Elephantulus*) from Profs. Elliot Smith (57) and Le Gros Clark (12, 13, 14), I have failed to find any mention of the cavum in these animals. In view of the important position occupied by this group in primate phylogeny (59), this is cause for regret. We do know, however, that a cavum is absent in *Talpa* (22), and as there is good reason for believing that the Insectivora (and the Menotyphla in particular) have preserved a number of primitive mammalian characteristics, the assumption seems warranted that the solid septum in the mole is a feature in point.

We are fortunate in possessing Prof. Elliot Smith's (56) excellent description of the open cavum in *Tarsius* and evidence that that animal is a close relative

of the form which was ancestral to all the higher Primates (72). Moreover, the microsmatic condition which characterises the latter animals and has exerted so profound an influence upon their cerebral anatomy is already present in *Tarsius* (56); thus it would seem as though the closed cavum of the higher Primates were derived from the open cavum of a tarsioid (or, at any rate, a primitive Primate) ancestor. Clearly the open cava of the highly specialised Carnivora and Rodentia, and even of the Edentata, are far removed from the line of evolution of the human cavum, as is the closed cavum of the horse (if it exists), but the like can scarcely be said of the open cava of *Tarsius* and of *Macacus*.

It seems to me that two divergent phylogenetic lines may be discerned in the history of the cavum septi pellucidi.

On the one hand, the primitive mammalian solid septum (represented in the Metatheria) gave origin to the open cavum of the "typical" Mammals—Carnivora, etc.

On the other hand, the primitive mammalian solid septum (represented in the Metatheria) gave rise to the primitive insectivoroid solid septum (represented in *Talpa*); from this arose the primitive Primate or tarsioid open cavum (represented in *Tarsius*), whence, finally, was evolved the closed cavum of the higher Primates (represented in *Homo*).

What are the phylogenetic factors responsible for the conversion of the open cavum into that which is closed? This question has been answered by Prof. Elliot Smith. Concomitantly with the pallial expansion which characterises the evolution of the Primates, the great pallial commissure, the corpus callosum, increases enormously and "develops its genu, which increases in extent in the higher Mammalia, until in Man it completely shuts off the 'cavum septi' from the surface" (52)[1].

VII. SUMMARY

1. Personal investigations are recorded which show that certain statements that have been made as to the absence of the cavum septi pellucidi in the rabbit, cat and dog are incorrect. These animals do possess a cavum, as does the macaque monkey.

2. The observations in question, together with others recorded in the literature, show that the generalisation that the cavum septi pellucidi is closed wherever it occurs is likewise incorrect.

3. Amongst the Mammalia the cavum may be absent, as in the mole, or present, as in Man; when present it may be open, as in the cat and the macaque, or closed, as in Man.

4. The available evidence concerning the ontogeny and phylogeny of the two types of cavum (open and closed) is reviewed and discussed. It is concluded that the best evidence favours the view that the closed cavum (of Man) develops by interstitial cleavage in the lamina terminalis.

[1] I beg to thank Prof. Elliot Smith for kind permission to quote so extensively from his writings.

5. A diphyletic theory of the evolution of the cavum septi pellucidi is suggested, namely, that on the one hand the primitive mammalian solid septum pellucidum gave origin to the open cavum of the "typical" Mammals, whilst on the other hand the primitive mammalian solid septum gave rise to the primitive insectivoroid solid septum, from which arose the primitive Primate open cavum, whence finally was evolved the higher Primate closed cavum. The probable factors involved in these changes are briefly discussed.

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THE MECHANOSTRUCTURE OF THE PERICARDIUM[1]

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I. INTRODUCTION

In the literature, as far as we know, the structure of the pericardium is hardly considered, and enough attention has not been paid to the orientation of collagen fibres within the pericardium. A. MacAlister (1) says: "In structure the parietal layer of the pericardium consists of two almost inseparable strata, an outer fascial layer composed of *several laminae of mostly longitudinal white and yellow fibres*, continuous into the sheaths of the vessels which pierce it, and an inner representing a serous membrane. . ., etc."

Rauber-Kopsch (2), Henle (3), Poirier (4), Testut (5), Cruveilhier (6), Sappey (7), and in general all the authors of text-books, consider the pericardium as being a fibrous structure built up of fibres orientated in all directions. The connections of the pericardium with the diaphragm and blood vessels (aorta, pulmonary artery) are mentioned in every anatomy book. In the old treatises only MacAlister (1) mentions the longitudinal orientation of fibres which are arranged in "several laminae," and Bourgery (8) draws attention to the reflection of some of these longitudinal fibres into the adventitia of the blood vessels. Braus (9), while discussing some physiological aspects of the pericardium, considers the structure of this membrane rather superficially. Little attention has been paid by students to the structure of the pericardium, the majority of papers dealing mostly with the connections of the pericardium and with its suspending ligaments (10–18). Recently the study of the relations of the pericardium to the activity of the heart, and the progress of the surgery of this membrane, have stimulated a closer consideration of its anatomy (19–22); but nowhere is the structure of the pericardium studied in the light of modern

[1] This is a part of a series of studies which one of us started six years ago. These studies are concerned with the orientation of connective tissue. The first study published in this series is entitled: Gr. T. Popa, "Structure fonctionnelle de la dure-mère crânienne avec considérations générales sur les facteurs mécaniques crâniens chez les Vertébrés en général et chez l'homme en particulier," *Annales Scientifiques de l'Univ. de Jassy*, t. XIII, p. 119. In this paper a full list of references to the subject is published, and the meaning of the term "functional structure" is considered. As the expression "functional structure" is used in connection with various structures distinct from connective tissue and its function (for instance, the structure of various glands: W. Berg, "Ueber funktionnelle Leberstrukturen I, II," *Arch. f. mikrosk. Anatomie*, 1920, Bd. XCIV, p. 518; 1922, Bd. XCVI, p. 54), we shall use the more appropriate term of "*Mechanostructure*," meaning by this term that the factors which determine the functional activity and, through it, the structure of fibrillar connective tissue, are of a mechanical kind: the foremost in importance being traction in opposite directions.

ideas on functional structure, as defined in the works of Hermann Mayer (23–24), Julius Wolff (25–26) and W. Roux (27).

II. DESCRIPTION OF MECHANOSTRUCTURE

1. Ligaments of the pericardium

A. *Ligamenta sterno-pericardiaca*

These are two in number and are quite accurately described in various text-books (Testut (5), vol. II, p. 157). Poirier (4) calls them also Luschka's ligaments, and agrees with this author that the rôle played by these ligaments is that of suspending the pericardium both in the vertical and horizontal positions of the body (superior ligament, *loc. cit.* p. 619), and of suspending the pericardium only in the horizontal position of the body (inferior ligament, *loc. cit.* p. 619; *see also* Luschka (28)). The superior ligament is also called ligamentum sterno-costo-pericardiacum and the inferior is also called ligamentum xipho-pericardiacum. Besides playing this static rôle these ligaments have in the opinion of physiologists and surgeons a dynamic function related to the activity of the thorax during the act of respiration (Brauer und Fischer (19), p. 1844).

These ligaments show a definite grouping of their fibres, thus indicating the direction of mechanical forces working in relation to them.

Two groups of fibres take origin from the superior end of the sternum on the anterior aspect of the pericardium below the large vessels of the heart, and they intermingle with the other fasciculi (figs. 1 and 2) in the wall of the pericardium. These fibres correspond to the superior ligament of Luschka. Another bundle comes from the xiphoid process and ascends towards the anterior wall of the pericardium; it seems to correspond to the inferior ligament of Luschka (ligamentum sterno-pericardiacum inferius; fig. 1). These three bundles are orientated in opposite directions and in between them in many cases there is only a lax connective tissue. Sometimes one can distinguish another group of fibres coming from the middle part of the sternum and the neighbouring costal cartilages, crossing the end of the superior bundle, and having an antero-posterior orientation (fig. 1). In this case, a continuous layer of orientated fibres connects the sternum with the anterior wall of the pericardium, into which these fibres enter and intermingle with the other fibres of this structure.

B. *Ligamenta phreno-pericardiaca*

The usual description of these ligaments does not appear to us to be quite accurate. The text-books distinguish an anterior ligament and two lateral ones; the latter are called also the ligaments of Teutleben (Poirier (4), p. 620). We shall consider Teutleben's ligaments together with the dorsal longitudinal fibre bundles of the pericardium; as for the anterior phreno-pericardial ligament we distinguish various bundles of collagen fibres which come from

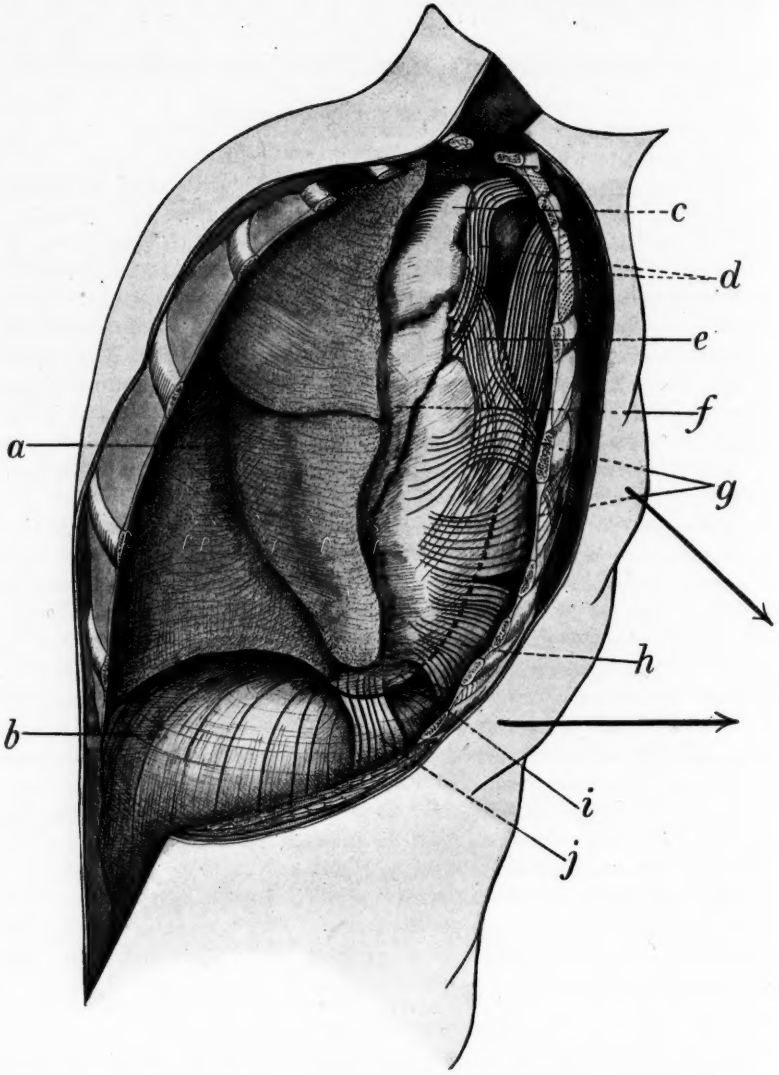

Fig. 1. Ligamenta sterno-pericardiaca with their mechanostructures. (Human.)
a, pulmo dexter; *b*, diaphragma; *c*, arcus aortae; *d*, ligamentum sterno-pericardiacum superius; *e*, fasciculus aortico-apicalis; *f*, atrium dextrum; *g*, ligamentum sterno-pericardiacum medium; *h*, ligamentum sterno-pericardiacum inferius; *i*, apex cordis; *j*, ligamentum phreno-apicale.

the sterno-costal part of the diaphragm and enter the anterior wall of the pericardium. They are arranged in groups across the anterior line of connection between the diaphragm and the pericardium, and they spread out divergently into this membrane and can be followed superiorly into the adventitial layer of the aorta and pulmonary artery. They are arranged in several superimposed layers and generally follow two principal directions: one to the pulmonary artery and the other to the aorta (fig. 5, fasciculus phreno-anonymus and fasciculus phreno-pulmonalis). In the majority of cases these fibres were arranged in three fairly distinct groups which we called: (1) ligamentum phreno-pericardiacum anterius sinistrum (fig. 2, near to the apex cordis); (2) ligamentum phreno-pericardiacum anterius medium (fig. 2); and (3) ligamentum phreno-pericardiacum anterius dextrum (fig. 2) in front of the vena cava inferior, which might be confused with the so-called Teutleben's right ligamentum phreno-pericardiacum laterale. There is no evident gap between these three groups of fibres, but because of their upper connections they show a definite functional and possibly morphological separation. These ligaments must be considered together with the fibres which pass from the various large blood vessels of the heart into the anterior wall of the pericardium, thus producing one and the same system of trajectorial lines of force; the function of these fibres will be considered later.

C. *Ligamentum vertebro-pericardiacum*

Such a ligament is described in all anatomy books, and some authors call it also the ligament of Béraud. This author described it as ligamentum superius pericardii (29). The description given by Béraud does not agree with that of Teutleben, and Testut denies the existence of such a ligament as described by the former authors. We believe also that a true vertebro-pericardial ligament does not exist, but there is a very important group of longitudinal fibres placed on the dorsal side of the pericardium which might be taken for such a ligament. Its detailed description will follow later on.

2. Fibres in the pericardium

Up to the present nobody has examined the fibrous structure of the pericardium and its differentiation in relation to its function, because the idea of mechanostructure has been developed only recently. In certain books we find some details concerning the general arrangement of fibres in the pericardium, for instance in MacAlister (1), p. 318. Bourgery (8) relates some old observations of Malpighi who found that long fibres, which he called "muscle-fibres," descend from the base to the tip of the pericardium. The same observation, as related by Bourgery, was made by Lancisi, who observed also, besides the longitudinal fibres, some other fibres running transversely in such a way that "their crossing produces a kind of reticulum resembling that of muscular membrane of the bladder" (p. 31, *loc. cit.*). Bourgery does not decide on

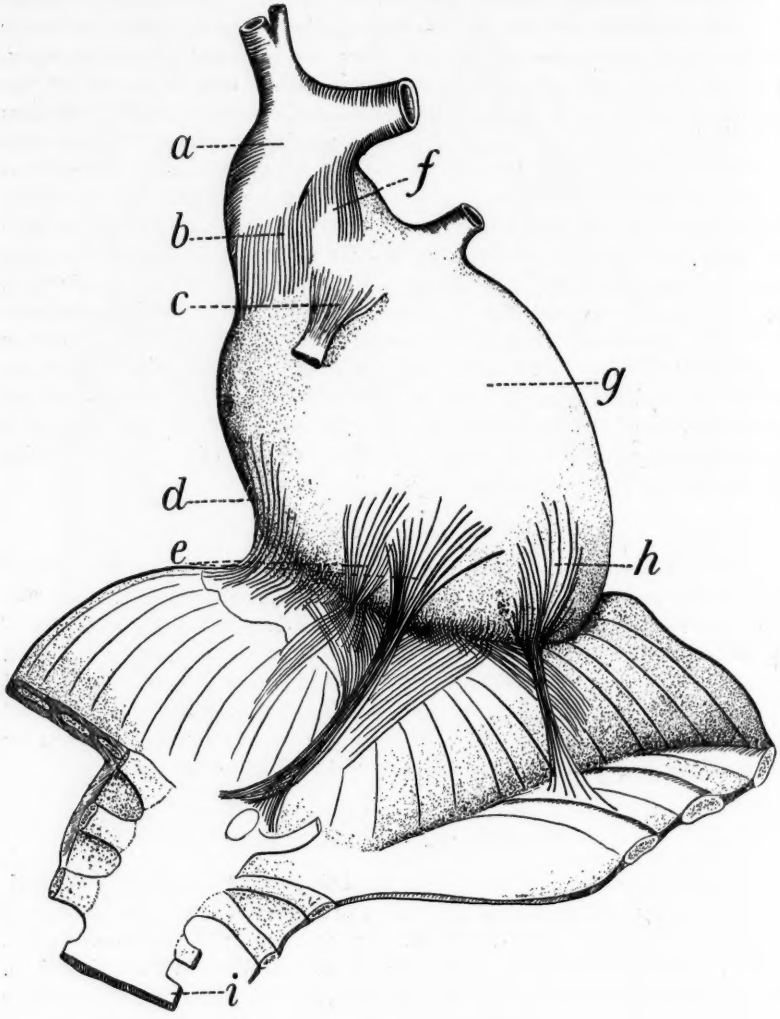

Fig. 2. Ligamenta anteriora pericardii. (Human.)

a, arcus aorticus; *b*, fibrae inter-arteriales; *c*, ligamentum sterno-pericardiacum superius; *d*, ligamentum phreno-pericardiacum anterius dextrum; *e*, ligamentum phreno-pericardiacum anterius medium; *f*, arteria pulmonalis; *g*, facies anterior cordis; *h*, ligamentum phreno-pericardiacum anterius sinistrum; *i*, sternum.

the nature of this lamina of fibres, but he confirms its existence. In a paper of Lacroix (30) it is stated that the pericardium is built up by "superposition of

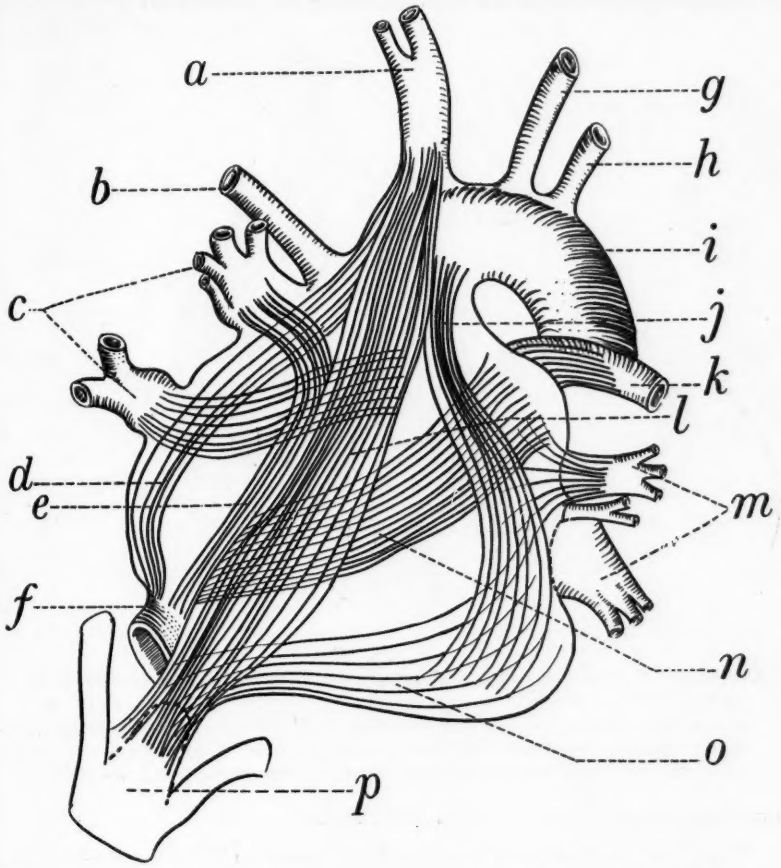

Fig. 3. Heart and vessels with the mechanostructures of the pericardium projected upon them. The lower end of the processus xiphoideus is reversed (anterior aspect). (Human.)

a, arteria anonyma; *b*, ramus dexter arteriae pulmonalis; *c*, venae pulmonales dextrae; *d*, fasciculus cavo-anonymus; *e*, fasciculus cavo-pulmonalis; *f*, vena cava inferior; *g*, arteria carotis communis sinistra; *h*, arteria subclavia sinistra; *i*, arcus aortae; *j*, fasciculus aortico-apicalis; *k*, ramus sinister arteriae pulmonalis; *l*, fasciculus xipho-anonymus; *m*, venae pulmonales sinistrae; *n*, fibrae transversae anteriores; *o*, fasciculus xipho-apicalis; *p*, processus xiphoideus.

bundles of fibres arranged in a number of layers" (quoted from Poirier (4), p. 627).

We distinguish two principal layers of fibres which are thin in the anterior wall of the pericardium and very thick in the posterior wall. We shall describe

what one can see after fine dissection of the external aspect of the pericardium (ventral and dorsal sides), and afterwards what one can see on the interior aspect (ventral and dorsal sides) after opening the pericardium.

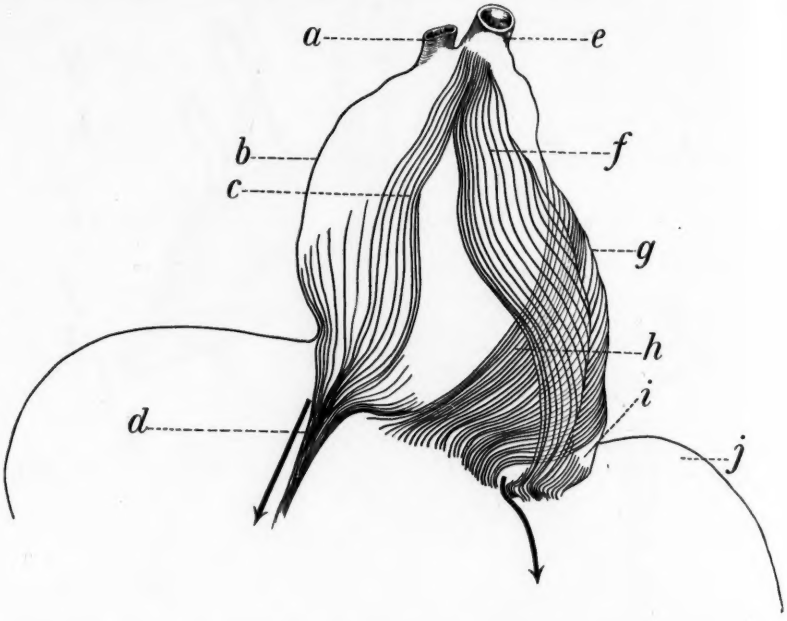

Fig. 4. Outlines of pericardium and of diaphragm. Ventral view. The mechanostructures projected upon pericardium. (Human.)

a, vena cava superior; *b*, margo dexter cordis; *c*, fasciculus phreno-aorticus dexter; *d*, ligamentum phreno-pericardiacum anterius; *e*, aorta ascendens; *f*, fasciculus phreno-aorticus sinister; *g*, margo sinister cordis; *h*, ligamentum phreno-apicale; *i*, apex; *j*, diaphragma.

(*a*) *Ventral aspect*

A. *Outer layer*

The principal direction of fibres in the pericardium is the longitudinal one. A very important bundle of fibres passes from the processus xiphoideus along the anterior wall of the pericardium up to the arteria anonyma. We called this bundle the fasciculus xipho-anonymus (fig. 3), and its fibres are intermingled with those of a deeper bundle connecting the centrum tendineum with the arcus aortae (fasciculus phreno-aorticus dexter, fig. 4), and with some other fibres which continue farther on (fasciculus phreno-anonymus, fig. 5). At the same level but directed towards the tip of the heart there is another bundle of longitudinal fibres descending from the arcus aortae and spreading on the ventral side of the pericardium (fasciculus aortico-apicalis, fig. 3). This last fasciculus is deep to and crosses a more superficial one which connects the centrum tendineum with the anterior wall of the pericardium up to the apex

cordis (ligamentum phreno-apicale, fig. 4). Still more superficially another large bundle connects the arcus aortae with the centrum tendineum (fasciculus phreno-aorticus sinister, fig. 4) and also the arteria pulmonalis with the centrum tendineum (fasciculus phreno-pulmonalis anterior, fig. 5).

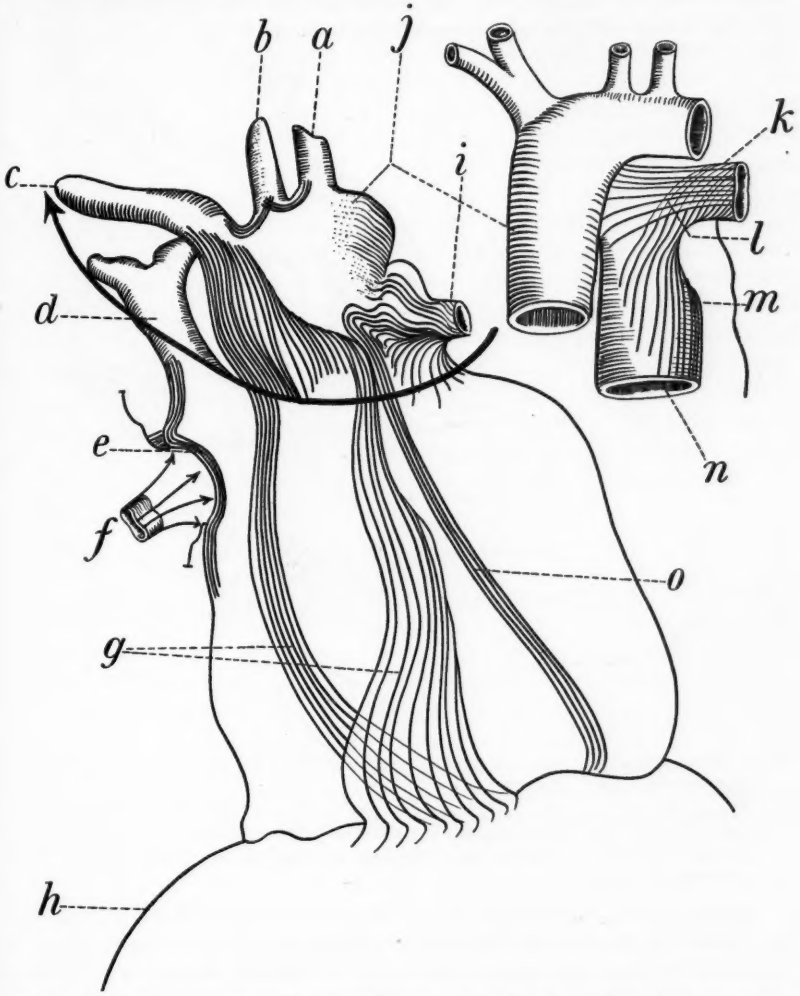

Fig. 5. Heart and vessels with some mechanostructures of pericardium projected upon its ventral aspect. (Human.)

a, arteria subclavia sinistra; *b*, arteria carotis communis sinistra; *c*, arteria anonyma; *d*, vena cava superior; *e*, annulus arteriae pulmonalis; *f*, ramus dexter arteriae pulmonalis; *g*, fasciculus phreno-anonymus; *h*, diaphragma; *i*, ramus sinister arteriae pulmonalis; *j*, aorta ascendens; *k*, ramus sinister arteriae pulmonalis; *l*, fibrae interpulmonales rectae; *m*, fibrae interpulmonales ascendentes; *n*, arteria pulmonalis; *o*, fasciculus phreno-pulmonalis anterior.

On the left side of the pericardium, in front of the pulmonary vessels, there is a small bundle descending from the aorta ascendens towards the left edge of the pericardium (fasciculus aortico-cardiacus, fig. 6). On the right side of the pericardium a longitudinal bundle of fibres connects the vena cava inferior with the arteria anonyma (fasciculus cavo-anonymus, fig. 3) and with the venae pulmonales (fasciculus cavo-pulmonalis, fig. 3).

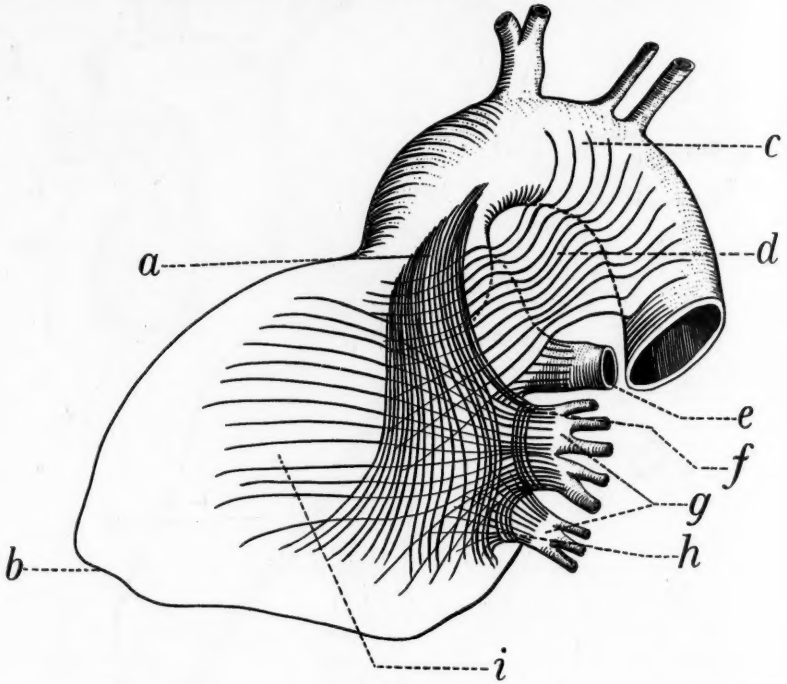

Fig. 6. Heart and vessels with some anterior mechanostructures of pericardium projected upon them (lateral aspect). (Human.)

a, fasciculus aortico-cardiacus; *b*, apex; *c*, arcus aortae; *d*, ligamentum cardio-aorticum; *e*, ramus sinister arteriae pulmonalis; *f*, annulus venae pulmonalis sinistrae superioris; *g*, venae pulmonales sinistrae; *h*, annulus venae pulmonalis sinistrae inferioris; *i*, fasciculus transversus pericardiacus anterior.

Between all these longitudinal bundles of fibres there are fibres in an oblique or transverse plane connecting them in various directions (fibrae transversae anteriores, fig. 3; fibrae xipho-apicales, fig. 3). Starting from each pulmonary vein, bundles of fibres spread underneath and between all the above-described bundles (figs. 3 and 6). An outstanding feature in this complicated arrangement is also the constant existence of a thick and large bundle of fibres connecting the anterior wall of the pericardium with the arcus aortae (ligamentum cardio-aorticum, fig. 6). This ligament is completely blended with the well-known ductus arteriosus, which is itself fibrous. Finally we find quite clearly

defined, although not so obvious as when seen from within the pericardium, systems of circular fibres round every pulmonary vein producing inextensible rings around every venous orifice (figs. 5 and 6).

(*b*) *Dorsal aspect*

The collagen fibres are extremely thick and grouped in large bundles generally directed longitudinally. Nearly all the bundles spread from a small area lying behind and a little to the right of the vena cava inferior. In this area the fibres are continuous with the centrum tendineum, and many groups of fibres might be considered actually as tendons of the diaphragm. Probably some of these fibres were considered as a ligament, and, by the confusion of orientated connective tissue with lax tissue, a long bundle came to be described as the vertebro-pericardiac ligament (especially Teutleben's left ligament). In fact we find long tracts of fibres ascending up to various levels and producing loops around the pulmonary veins and arteries. The longest fibres pass up to the arcus aortae and the bronchi. And so we differentiate the following groups: fasciculus centro-atrialis sinister (fig. 7), fasciculus centro-atrialis dexter (fig. 7), fasciculus centro-aorticus, and fasciculus centro-trachealis. Besides these we find two other thick bundles connecting the centrum tendineum with the posterior and left wall of the pericardium: fasciculus centro-cardiacus I and fasciculus centro-cardiacus II (fig. 7). The fibres of both fasciculi cross nearly at right angles into the pericardium.

B. *Inner layer*

(*a*) *Ventral aspect*

In this place there are very few fibres, and almost all are mere extensions from the posterior and lateral walls of the pericardium. We can follow the prolongation of a long bundle of fibres from the posterior wall (fasciculus phreno-trachealis, fig. 8) into the posterior surface of the anterior wall of the pericardium. Similarly we can follow the extension of some fibres running more or less transversely and coming from the left side of the pericardium: fibrae arciformes posteriores. Generally it is noticed that, whereas on the anterior aspect of the ventral wall of the pericardium the fibres are orientated chiefly in a longitudinal direction, on the dorsal aspect of this wall they are almost all running transversely.

(*b*) *Dorsal aspect*

The structure of the pericardium exhibits its greatest complexity in this region. With careful dissection one can distinguish many layers of fibres superimposed in a definite arrangement. Three categories of bundles can be defined: *longitudinal, transverse* and *circular.*

(1) *Longitudinal fibres.* A long tract of fibres descends from the trachea between the right and left pulmonary veins, passes near and to the left of the vena cava inferior, and extends through the diaphragmatic portion of the

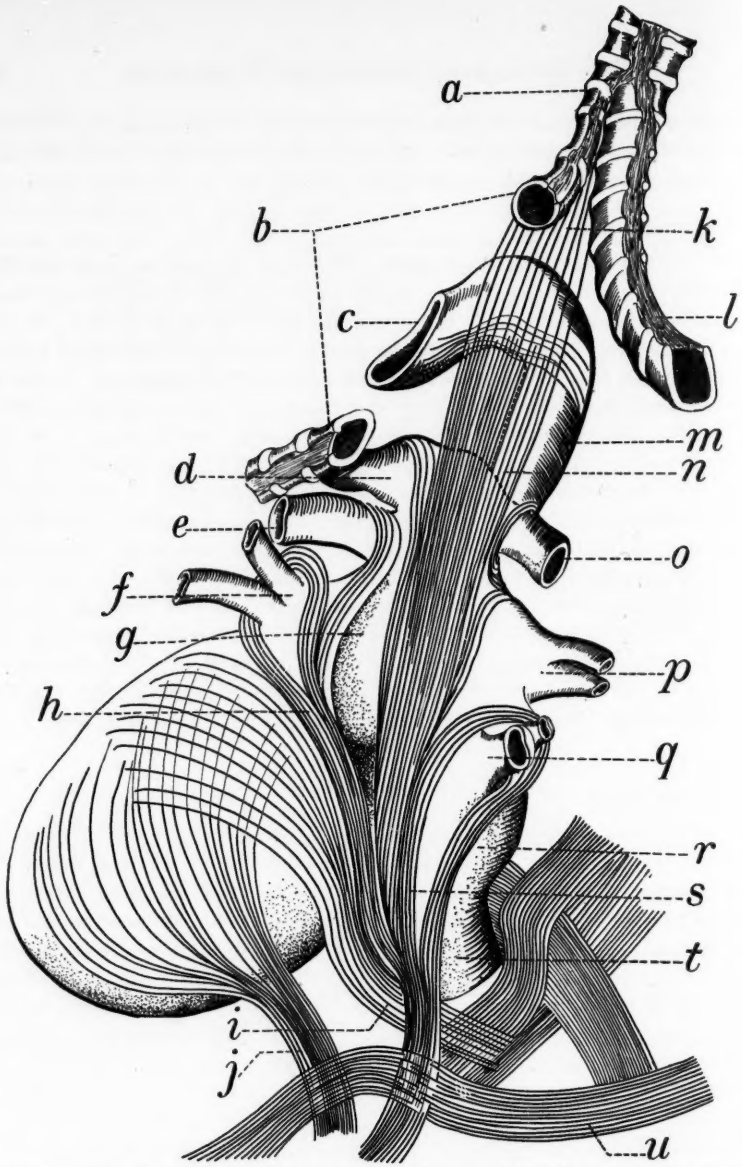

Fig. 7. Dorsal aspect of the heart and vessels on which are projected the mechanostructures of the pericardium in their principal features on the dorsal side. (Human.)

a, trachea; *b*, bronchus sinister; *c*, arcus aortae; *d*, ramus sinister arteriae pulmonalis; *e*, vena pulmonalis sinistra superior; *f*, vena pulmonalis sinistra inferior; *g*, atrium sinistrum; *h*, fasciculus centro-atrialis sinister; *i*, fasciculus centro-cardiacus I; *j*, fasciculus centro-cardiacus II; *k*, fasciculus centro-trachealis; *l*, bronchus dexter; *m*, aorta descendens; *n*, fasciculus centro-aorticus; *o*, ramus dexter arteriae pulmonalis; *p*, vena pulmonalis dextra superior; *q*, vena pulmonalis dextra inferior; *r*, atrium dextrum; *s*, fasciculus centro-atrialis dexter; *t*, vena cava inferior; *u*, fasciculus intraphrenicus.

pericardium up to its anterior wall (fasciculus phreno-trachealis, fig. 8). Another group of fibres descends between the right pulmonary veins, and, near the vena cava inferior, changes its direction to become transverse (annulus periatrialis (fibrae dextrae), fig. 8). Behind the fasciculus phreno-trachealis there is a large fasciculus which connects both bronchi with that part of the pericardium lying over the apex cordis (fasciculus broncho-apicalis,

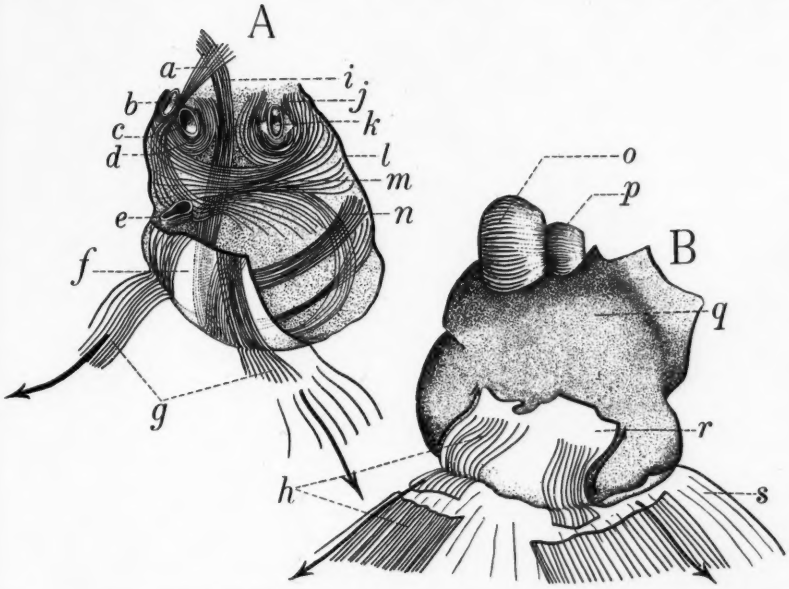

Fig. 8. A. Posterior wall of pericardium with some mechanostructures on it. B. Posterior wall of pericardium without mechanostructures and the directions of fibres in the ligamentum phreno-pericardiale. (Human.)

a, annulus periatrialis (fibrae dextrae); *b*, vena pulmonalis superior et dextra; *c*, vena pulmonalis inferior et dextra; *d*, annulus venae pulmonalis dextrae; *e*, vena cava inferior; *f*, paries anterior pericardii; *g*, ligamentum phreno-pericardiale anterior; *h*, ligamentum phreno-pericardiale anterior; *i*, fasciculus phreno-trachealis; *j*, annulus venae pulmonalis sinistrae; *k*, vena pulmonalis sinistra inferior; *l*, paries posterior pericardii; *m*, fibrae transversae posteriores; *n*, fibrae arciformae posteriores; *o*, aorta ascendens; *p*, arteria pulmonalis; *q*, paries posterior pericardii; *r*, paries anterior pericardii; *s*, diaphragma.

fig. 9). Some of these fibres do not reach the apex cordis but end in front of the vena cava inferior (fibrae verticales, fig. 10). From the posterior side of the vena cava inferior, bundles of fibres ascend in front of or behind various components of the right hilum (fibrae cavo-pulmonales superiores; fibrae cavo-hilares et bronchiales dextrae; fibrae cavo-pulmonales inferiores, figs. 9 and 10). Some fibres unite together both venae cavae (fibrae intercavae, fig. 10). Several bundles, more or less vertical, become horizontal at their

caudal end and form together large rings which we call "periatrial," because of their position just between the atria and ventricles of the heart (fasciculus cavo-dorsalis, fig. 9; annulus periatrialis (fibrae dextrae and fibrae sinistrae), fig. 10; fasciculus aortico-periatrialis, fig. 11).

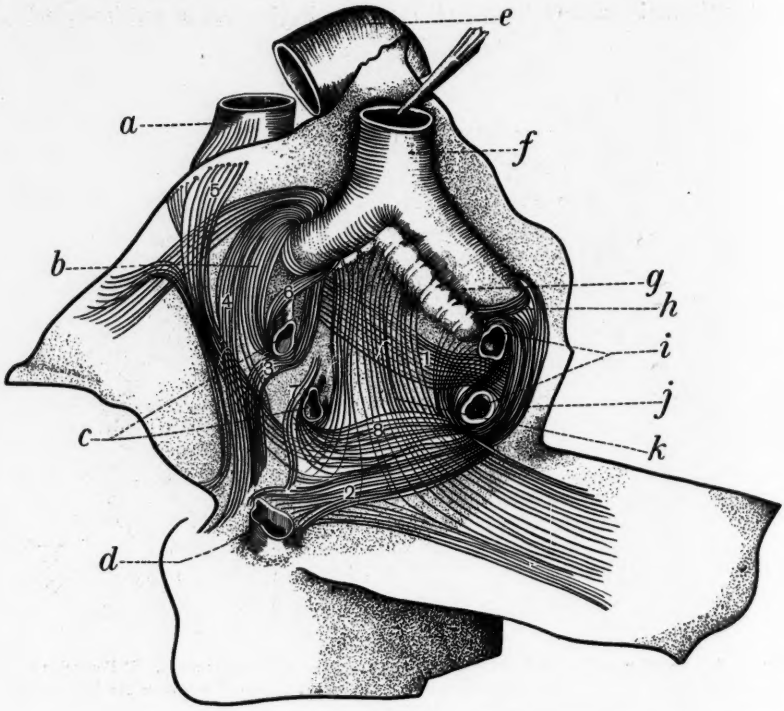

Fig. 9. Dorsal wall of pericardium with its principal mechanostructures (frontal view). (Human.) *a*, vena cava superior; *b*, annulus perihilaris; *c*, venae pulmonales dextrae; *d*, vena cava inferior; *e*, arcus aortae; *f*, arteria pulmonalis; *g*, bronchus sinister; *h*, annulus periarterialis sinister; *i*, venae pulmonales sinistrae; *j*, annulus perihilaris; *k*, fasciculus broncho-apicalis. 1, fibrae transversae interhilares posteriores; 2, fibrae cavo-hilares sinistrae; 3, fibrae cavo-hilares et bronchiales dextrae; 4, fibrae cavo-pulmonales superiores; 5, fasciculus cavo-dorsalis; 6, annulus venae pulmonalis dextrae et superioris; 7, fibrae cavo-pulmonales inferiores; 8, fibrae transversae infrahilares.

(2) *Transverse fibres.* A group of fibres unites the roots of the lungs (fibrae transversae interhilares posteriores, fig. 9), some others are present at the same level but below the roots (fibrae transversae infrahilares, fig. 9), and lower down a group of fibres spreads transversely from the vena cava inferior (fibrae cavo-hilares sinistrae, fig. 9; et dextrae, fig. 11). On an anterior plane there is another bundle between the roots of the lungs (fibrae transversae interhilares

anteriores, fig. 11). In front of this complex of fibres there is another group which, after crossing the posterior wall of the pericardium, bends to the right and left, entering the lateral walls of the pericardium (fibrae transversae arciformes, fig. 11).

At the bifurcation of the pulmonary artery there are two small bundles of fibres which connect each branch with the posterior wall of the pericardium

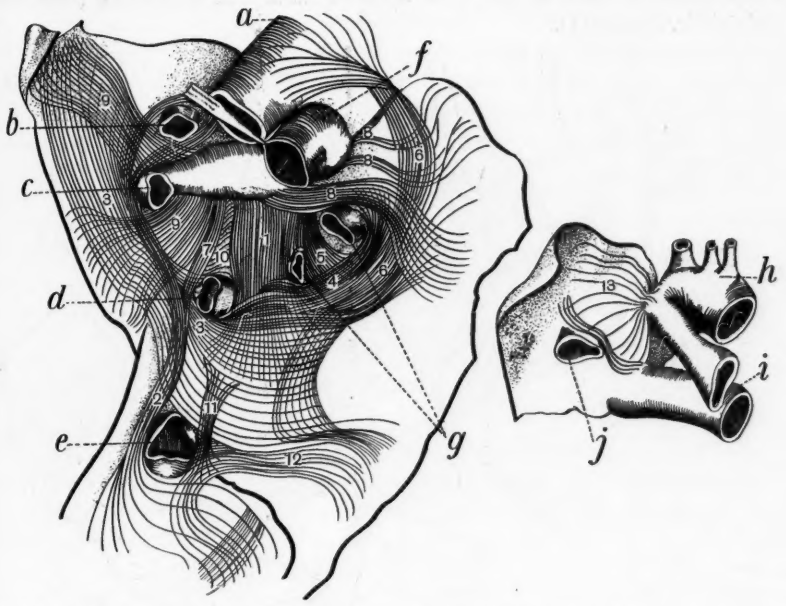

Fig. 10. Posterior wall of pericardium with its mechanostructures. (Human.)

a, arcus aortae; *b*, vena cava superior; *c*, arteria pulmonalis dextra; *d*, venae pulmonales dextrae; *e*, vena cava inferior; *f*, arteria pulmonalis sinistra; *g*, venae pulmonales sinistrae; *h*, arcus aortae; *i*, arteria pulmonalis; *j*, vena cava superior. 1, fibrae verticales; 2, fibrae intercavae; 3, annulus periatrialis (fibrae dextrae); 4, annulus periatrialis (fibrae sinistrae); 5, annulus peripulmonalis sinister; 6, fasciculus aortico-periatrialis; 7, fibrae cavo-hilares dextrae; 8, fibrae phreno-pulmonales sinistrae; 9, fibrae phreno-pulmonales dextrae; 10, fibrae transversae interhilares posteriores; 11, fibrae cavo-pulmonales inferiores; 12, fibrae cavo-apicales; 13, fibrae phreno-aorticae.

(fibrae phreno-pulmonales dextrae and sinistrae, fig. 10). In the same way the arcus aortae is fixed to the lateral wall of the pericardium by a bundle of fibres (fibrae phreno-aorticae, fig. 10). In this transversely orientated group of fibres terminate many oblique or vertical fibres which contribute to the formation of the periatrial rings (figs. 9–11).

(3) *Circular fibres.* The only note on these fibres that we found in the literature was that of Luschka (31). He mentions that they are found around the pulmonary veins and that they are very thick.

In actual fact this system of fibres is more complicated. We distinguished, around every pulmonary vein, strong rings (figs. 8, 9, 11) which are seen also sometimes outside the pericardium (fig. 6). We also found strong rings round the pulmonary arteries (fig. 9) and long fibres round the roots of the lungs (annulus perihilaris, figs. 9 and 11), and, continuing farther on, still longer fibres are grouped in a very large and thick ring which surrounds the whole pericardium in front of the limit between atria and ventricula (annulus periatrialis, figs. 9–11).

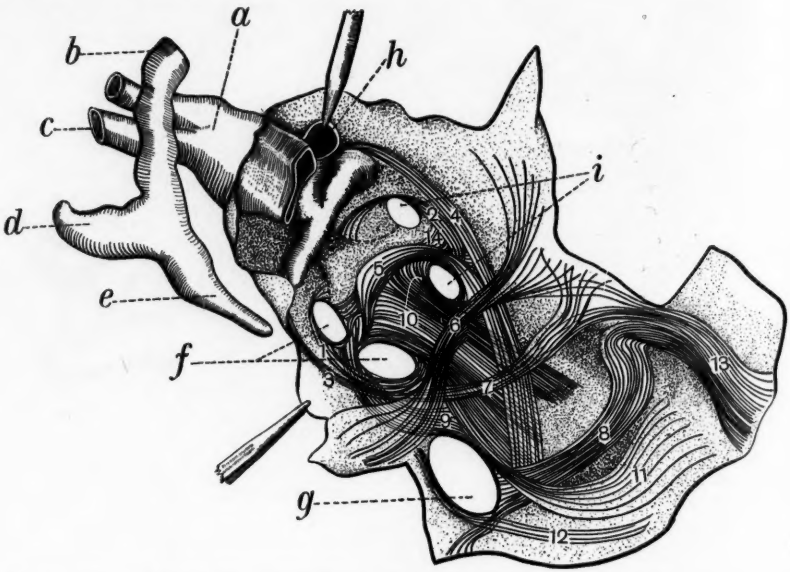

Fig. 11. Posterior wall of pericardium with its mechanostructures. (Human.)
a, arcus aortae; *b*, vena anonyma sinistra; *c*, arteria anonyma; *d*, vena anonyma; *e*, vena cava superior; *f*, venae pulmonales dextrae; *g*, vena cava inferior; *h*, arteria pulmonalis; *i*, venae pulmonales sinistrae. 1 and 3, annulus perihilaris dexter; 2, annulus perihilaris sinister; 4, annulus periatrialis (fibrae sinistrae); 5, fibrae transversae interhilares anteriores; 6, fibrae transversae arciformes; 7, annulus periatrialis (fibrae dextrae); 8, fasciculus cavo-apicalis; 9, fibrae cavo-hilares; 10, fasciculus broncho-phrenicus; 11, fasciculus broncho-apicalis; 12, fibrae cavo-apicales; 13, ligamentum phrenico-apicale; 14, fibrae transversae interhilares posteriores.

III. THE MECHANICAL FACTORS WHICH MIGHT EXPLAIN THE ORIENTATION OF FIBRES IN THE PERICARDIUM

All movements of the thorax are related to two great functions: respiration and the attitude of the erect body. These movements are also the factors which determine the position of the pericardium and its state of tension. We shall call these the "*extrinsic*" mechanical factors. But the pericardium is a sac containing a heart which is continuously changing its volume by reason

of its rhythmic function, and the position of the heart inside the pericardium depends largely upon posture. We shall call these various factors, by means of which the beating heart influences the pericardium, the "*intrinsic*" mechanical factors.

A. Extrinsic mechanical factors

1. *Respiration*

The movements of respiration are accomplished by changes occurring in the walls of the thorax. These changes concern especially the diaphragm (caudal wall) and the sterno-costal wall (antero-lateral). The conditions under which the walls of the thorax move and their various modifications during respiration are carefully studied by Fick (32) (pp. 132–204) and by Braus (9) (Bd. I, pp. 210–20; Bd. II, pp. 674–86). The principal results of these movements are a rise of tension directed from the sternum and ribs to the anterior wall of the pericardium, and another group of tension rises from the diaphragm which pulls the pericardium downwards. The third group of tensions is produced by the pull of the roots of the lungs, which at every inspiration are pulled laterally and backwards by the dilating mass of the lungs. But while the pull of the roots of the lungs is equalised by the opposite directions in which they act, the pull of the diaphragm would be uncontested if at the opposite end the pericardium were free, but that is not the case. Opposite to the diaphragm the pericardium is fixed to the blood vessels: aorta, pulmonary artery and vena cava superior; and laterally it is also fixed to the pulmonary veins and bronchi. All these points oppose the diaphragm, and the longitudinal forces working through the pericardium are so balanced. In that way the pericardium is strongly fixed between four opposing points: transversely between the roots of the lungs, vertically between the diaphragm, the blood vessels, and, again, the roots of the lungs. Encircling these four points a strong connective tissue frame is built up, by which means the stronger the tension set up the better will be the protection for the heart. The pericardium in such conditions becomes absolutely rigid and appears like a hard bony membrane. To understand this it is enough to look at our figures. We see at once that the ligamentum sterno-pericardiacum superius (fig. 1) is extended by the manubrium sterni at every inspiratory movement and itself pulls the upper part of the pericardium upwards; on the other hand, by the same mechanism, the ligamentum sterno-pericardiacum inferius (fig. 1), stretched by the processus xiphoideus, pulls the lower part of the pericardium downwards at every inspiratory movement. In this way these ligaments are antagonistic and produce coincidentally a tension in the anterior wall of the pericardium; this tension is directed longitudinally in the pericardium, with a slight divergence backwards. With these two forces is associated, when it is present, the tension of the ligamentum sterno-pericardiacum medium, which pulls directly forwards. In the structure of these ligaments we found that the fibres were orientated

in the principal directions just described. So, besides the purely static rôle ascribed by Luschka (31, 33) to the sterno-pericardiac ligaments, we assign also a dynamic rôle.

Both ligaments which are antagonistic in the cranio-caudal direction are synergists when they transmit the traction of the sterno-costal wall to the pericardium in the dorso-ventral direction. In that case they work together and their common antagonist is represented by the dorsal connections of the pericardium with the diaphragm round the vena cava inferior (especially by fasciculus centro-cardiacus I, fasciculus centro-atrialis dexter, fig. 7; and by the ligamentum phreno-pericardiacum anterius dextrum, fig. 2).

The trajectorial lines of forces in this case pass from the upper left side of the pericardium to the right inferior side and posteriorly, crossing the anterior wall of the pericardium diagonally. The bundle called by us fibrae transversae anteriores (fig. 3) should be included in this system of long trajectories.

One can understand that the degree of tension in this system is extremely changeable and depends on the intensity of the respiratory movements. In rest, the activity of the thoracic wall is very slight and respiration is performed almost entirely by diaphragmatic movements alone. The diaphragm descends and ascends gently, the centrum tendineum being almost fixed. Yet, in these conditions, the system of trajectories above described is slightly extended because of thoracic rebound (experiment of Braune). Proportionately with the increased traction of the diaphragm and anterior thoracic wall in forced inspiration, the tension in this system of trajectories increases.

The descent of the diaphragm causes a still greater effect upon the pericardium after the forward and upward movement of the anterior wall of the thorax is accomplished. In these new conditions the "moment" of the diaphragm muscle is greatly increased. The power of pull in this muscle is augmented and the angle of incidence of the diaphragm upon the pericardium increases. The pull of the diaphragm is orientated in this case vertically and its greatest power is exerted on the dorsal side of the pericardium. Along this fibrous sac rise long trajectories of forces which are directed from the diaphragm up to the arcus aortae and to the arteria anonyma. These trajectories are shown very clearly in the longitudinal bundles already described (figs. 3, 4, 5, 6, 7). Considering them in their totality we find that they are grouped especially along four principal lines: one, which unites the arteria anonyma with the vena cava inferior (figs. 3, 4); second, that which unites the aorta and pulmonary artery with the left side of the centrum tendineum (figs. 3, 5); third, that which unites both vena cavae (fig. 10); and fourth (placed dorsally), which unites the centrum tendineum with the arcus aortae and the other large blood vessels (fig. 7). Between these four long sheets of resistant pericardium there are some less resistant zones. This may explain why in rupture of the pericardium the split is usually longitudinal (Hyrtl (34)). These longitudinal sheets of resistance provide an excellent support for the transverse bundles, and together they form a strong membrane well planned for resistance to every direction of pull.

Particularly important are the dorsal longitudinal bundles which fix a permanent distance between the bronchi (and the roots of the lungs as a unit) and the centrum tendineum (fig. 7). Fasciculus centro-aorticus, fasciculus centro-trachealis, and fasciculus centro-atrialis dexter et sinister (fig. 7) must be considered as an inextensible ligament which fixes a certain distance, always the same, between the roots of the lungs and the centrum tendineum. We had the opportunity of confirming this fact by means of the X-ray screen in the case of a child who had swallowed a little key which stopped in the right bronchus. Even in the deepest inspirations, combined with extension of the spine, the distance between bronchus and diaphragm remained the same. The roots and centrum tendineum ascended and descended together at every movement, like two structures firmly fixed to each other. This fact is of great importance in relation to the general function of the heart: the space destined to contain the atrial portion of the heart is inextensible and secures therefore a strong resistance to the internal pressure of blood, which could hardly be maintained by the thin muscular walls of the atria alone. This fact will be demonstrated more clearly when we consider the intrinsic mechanical factors.

These posterior longitudinal bundles of fibres (especially fasciculus centro-aorticus, fasciculus centro-trachealis and fasciculus centro-atrialis dexter (fig. 7)) are placed, if projected on the anterior wall of the pericardium, just behind the anterior longitudinal bundles (phreno-aorticus dexter, fig. 4; cavo-anonymus and cavo-pulmonalis, fig. 3). This general orientation of longitudinal fibres coincides to what is called the fixation line of the heart (Curschmann (35)). The clinical facts (L. Brauer und H. Fischer (19), p. 1844) recorded by surgeons and their hypotheses agree quite well with our morphological descriptions.

Transverse orientations. The lateral pull of the roots of the lungs is a very real and active force. At every inspiration the mass of the lungs following the expanding thoracic walls pulls the roots laterally and with them the walls of the pericardium. The roots are placed at the dorsal side of the pericardium and this portion especially will be subjected to the greatest extension. This fact explains the presence at this level of several strong bundles of fibres (fibrae transversae interhilares, fig. 9; fibrae transversae arciformes and fibrae transversae arciformes and fibrae transversae interhilares anteriores, fig. 11). By the same mechanism we explain the presence of strong bundles of fibres which connect the two bundles of the pulmonary artery to the pericardium (fibrae phreno-pulmonales sinistrae et dextrae, fig. 10). In the same way, bundles of fibres spread divergently in the wall of the pericardium from every pulmonary vein (fig. 3; fasciculus transversus pericardiacus anterior, fig. 6). All these transverse trajectorial systems indicate the line of pull of the pulmonary roots and associate themselves with the longitudinal systems above described, interweaving with each other in a complex unit continuously submitted to tractions which cross perpendicularly.

2. *Attitude of the erect body*

The mechanical factors (pull of roots) transversely orientated and those determined by the pull of the sternum are of importance at every moment in living Man, although with very great differences of degree. Those longitudinally active are important chiefly only in the extended position of the trunk. The extension of the trunk itself influences especially the anterior longitudinal tracts, where the traction becomes greater. The same extension alone relaxes somewhat the posterior longitudinal tracts (fig. 7) by causing dorsal displacement of the trachea. But, as the position of the body is never the sole factor

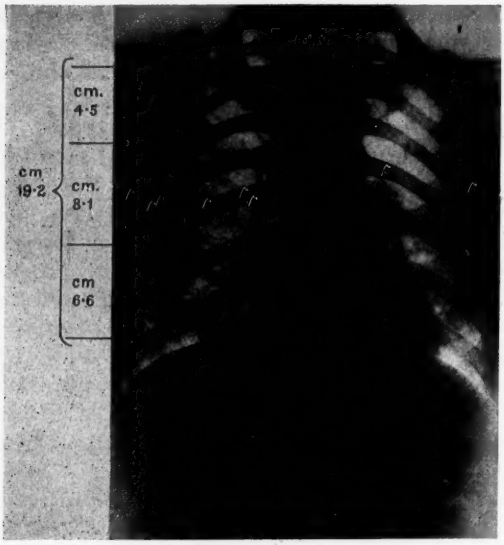

Fig. 12. Chest of an adult. End of normal expiration. Position of the body vertical.

at work, as soon as the inspiratory movements add their effect to that of the erect attitude the tension in the posterior ligaments increases continuously and is almost permanent. Conversely, in the flexed position of the trunk the anterior longitudinal ligaments are released and the posterior ligaments continue to be extended by means of the ventral inclination of the trachea. Therefore this fibrous bundle of the pericardium placed between the centrum tendineum and the bronchi is almost always tense and assures a constant position for the atrial portion of the heart. From these facts we conclude that the greatest stress exerted upon the pericardium coincides with a combination of maximum extension of the trunk with a forced inspiration. In this case the shape of the pericardium becomes more elongated and is quite narrow,

especially in its upper outline (fig. 13). On the contrary the greatest relaxation of the pericardium coincides with a combination of a maximum of body flexion with a forced expiration. In this case the shape of the pericardium becomes short and large, and its upper outline is thick. Within it the heart changes its inclination and tends to become almost horizontal (fig. 12). Between these two extreme positions occurs every intermediate one. As a result of such changes in the shape and position of the pericardium, the heart can move only laterally and vertically inside the pericardium. All these movements as a whole are made only by the apex of the heart, its base being

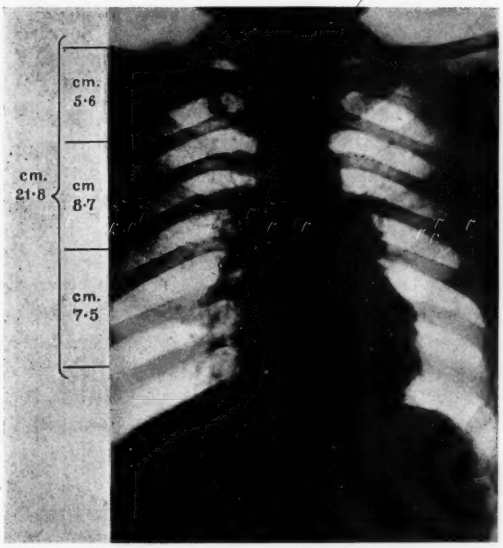

Fig. 13. Chest of an adult. End of forced inspiration. Position of the body in hyper extension.

strongly fixed. There is another point to be noted: the heart and pericardium are placed obliquely in a sagittal plane in such a way that they make a ventrally open angle with the direction of the trachea, and another angle with the vertebral column open caudally (Groedel (36)). At every flexion of the body the dorsal ligaments of the pericardium tend to become straight and move ventrally as a whole. This movement tends to force the ligaments anteriorly.

Summing up the extrinsic mechanical factors we find that the respiratory movements are working mostly in association with the movements of the body. The ventral inclination of the trunk is able to relax the longitudinal bundles of the pericardium to a certain degree. The dorsal inclination of the trunk on the contrary increases at every stage of the movement of the tension

in all the longitudinal ligaments. It is easy to understand how much the degree of tension in the pericardium varies under actions which demand more or less extension of the body, more or less muscular force and also more or less deep respiratory movements.

B. Intrinsic mechanical factors

All intrinsic factors are produced by the moving heart. The heart is an active organ which contains a fluid variable in quantity. The variability of blood mass causes a variability of weight. The points of incidence of this weight upon the pericardium vary also with the position of the body. Schematically we can compare the pericardium around the expansive mass of the heart as a fascia around a contracting muscle, and all increase of volume inside the pericardium will cause a rise in indirect tensions in the pericardium. These tensions will add their effects to those produced directly by the extrinsic factors. The oscillation of the heart's weight and volume is directly connected with the amount of blood contained during various phases of the heart beat and is affected by different complicated acts in which, by necessity, the circulation of the blood is influenced.

In every *systole* the heart becomes smaller and its weight naturally diminishes too; and it becomes larger and heavier during *diastole*. The *frequency of pulsation* is connected also with a change in volume. Generally a rapid rate is correlated with a diminution of heart volume, whereas deep slow contractions cause an increase of volume. Moritz (37) and Dietlen (38) observed a diminution of the heart's volume after exhausting work.

The *respiration* also influences the capacity of the heart. Holzknecht und Hofbauer (39) found that the heart enlarges during inspiration and becomes smaller during expiration. Contrary to these observations Moritz (40) found sometimes that the heart becomes smaller during inspiration. In this case, which is not universally admitted by all scientists, one might suppose that, besides the traction produced by the moving roots of the lungs, a great compressive power is set up by the expanding mass of the same lungs, acting upon the pericardium and heart. In all events when the respiration is associated with various movements of the body and with the closure of the glottis, as occurs so frequently in various actions (lifting of weights, forced pull, cough, defecation, etc.), the volume and capacity of the heart are greatly changed. All forced respiratory movements are grouped in two classes which correspond to the classical experiments of Müller and Valsalva. In the paper of Crowden and H. A. Harris (41) this influence is clearly shown. The same influences are demonstrated by Assmann (42).

The *total quantity of the blood in the body* influences directly the volume of the heart (Meyer, E. (43), Meyer und Seyderhelm (45)).

The *position of the body* influences also the heart volume (Dietlen (45), Moritz (46)).

The *position of the diaphragm*, itself a consequence of respiratory movements and of the attitude of the body, influences greatly the form and the volume of the heart.

The weight and volume of the heart is also under the continuous influence of the *muscle mass* of the body, *form of thorax*, *age*, *sex*, *body weight* and *body height*.

All these enormously varying groups of factors result in a continuous change in the behaviour of the heart which will press rhythmically on different points of the pericardium. This action of the heart determines the orientation of some fibres in the numerous circular bundles which resist maximal distension of the heart. Among these fibres there are two groups of special importance:

(*a*) Perivascular and perihilar rings (figs. 6, 8, 9);

(*b*) Periatrial rings (figs. 9, 10, 11).

(*a*) Under various influences the components of the roots of the lungs tend to separate them from each other up to certain limits. Against these centrifugal influences strong perihilar rings (fig. 9) hold together the pulmonary artery, pulmonary vein and bronchus. In addition, every pulmonary vein and pulmonary artery has a special ring which assures a constant opening at every moment of function (figs. 2, 8, 9). These rings protect the blood vessels, with their thin walls, against possible blood engorgement, and by their permanent extension through other groups of fibres fixed upon their periphery resist every tendency to closure by external pressure. By such a mechanism the blood coming and leaving the heart always finds the doors open at a constant diameter.

(*b*) The atrial walls are remarkably thin. The right auricle especially shows in its composition at certain places (musculi pectinati) thin walls built up only by endo- and epicardium between muscle fasciculi. Nevertheless the resistance of the wall at such places is not decreased. This fact is better understood if we consider the pericardium. It is around the auricle that the pericardium is strongest and the fasciculi of fibres are best developed. Furthermore, there are large fasciculi of fibres which encircle the thin walls of the auricles at their ventricular extremities (fasciculi periatriales dexter et sinister, figs. 10 and 11). This large and inextensible ring is prolonged backwards by the thick wall of the pericardium and plays the same rôle for the atria as the blood vessel rings for the pulmonary veins. It assures a constant space for the auricles. By its inextensibility it protects the auricles against over dilatation, and also, because of the close connections between this periatrial ring and the longitudinal bundles of fibres, it remains (in normal conditions) continuously extended and protects the thin walls of the auricles against the external pressure resulting from the increasing volume of the lungs during an acceleration of respiration movements.

Because of the relations of the heart with its pericardium only the ventricular portion of this moving organ can move inside the pericardial cavity. Thus, the change of position that takes place is a certain rotation of the heart

round its longitudinal axis, associated with the movement of the tip of the heart from left to right as is shown in fig. 5 (see direction of the arrow). We believe that there is a relationship between these rotatory movements of the heart and the direction of the ligamentum cardio-aorticum (fig. 6).

These intrinsic mechanical factors always work in association with the extrinsic ones. They cannot possibly be isolated. They add usually their effect to the action of extrinsic factors, working somewhat antagonistically. The general result is a state of high tension throughout the pericardium, increased during forced movements of the body and of the diaphragm, and released during flexion of the trunk and during shallow respiration.

IV. A FINE APPARATUS FOR BLOOD REDISTRIBUTION

It is well known that the total amount of the blood in the body is more constant in a certain individual than is the total amount of the blood in every separate organ. For instance, the quantity of blood in the lungs during inspiration is greater than during expiration. The quantity of blood in a muscle is ten times greater during intense contraction than during rest (Krogh(47)). This means that every change in the functional activity of an organ is associated with a change in the blood distribution in other organs, and that the total blood mass of the body is redistributed continuously between these various organs. This redistribution of blood is produced by a very simple mechanism: changes in diameter of the arteries causing the accumulation of blood in some organs and expulsion of blood from others. The alteration of calibre in the arteries has been considered up to now mostly as a result of vaso-motor balance. Besides this agency we found that the pericardium plays also an important mechanical rôle in the redistribution of blood by changing the size of large arteries merely by traction exerted upon the arcus aortae, arteria anonyma and carotis artery.

The pericardium is fixed to these blood vessels and to the diaphragm. At every inspiration the diaphragm is depressed and the superior aperture of the thorax is raised. The distance between these two points increases, and when extension movements of the body are associated with inspiration the distance is maximal and the blood vessels longest. In fig. 12[1] we present the radiogram of a chest in a vertical position during superficial respiration. Fig. 13 shows the same individual in hyperextension of the body and in forced inspiration. In the first condition the distance between the insertion of the pericardium upon the diaphragm and the first rib was 19·2 cm. The same distance is increased under the second condition to 21·8; that means a difference of 2·6 cm. between forced extension and a standing position of the body. In this difference we allow: 0·9 cm. for the heart (6·6 cm. vertical position,

[1] We are much indebted to Dr E. Radu, lecturer in Radiology at the Faculty of Medicine, University of Jassy, for all observations made on living bodies (60 individuals) by the X-ray screen and for taking the radiograms. We here express to him our best thanks.

against 7·5 cm. in forced extension); 0·6 cm. for the blood vessels inside the pericardium (8·1 cm. vertical, 8·7 cm. forced extension) and 1·1 cm. for the blood vessels outside the pericardium (4·5 cm. vertical, 5·6 cm. forced extension). The greatest increase in length takes place, therefore, in the arteria anonyma, left carotid artery and left subclavian. These arteries are large tubes through which a great amount of the total blood must pass at a certain time. If we suddenly change the size of these tubes the usual amount of blood will not be accommodated in the same time. As a result there are two possibilities: either the velocity of the blood circulation must increase (consequently the frequency of heart beat) or the blood mass must find its way somewhere else (in other words, a new redistribution of blood will take place).

We have controlled this theory by counting the radial pulse of 25 individuals in a horizontal position after complete rest. The pulse rate was first counted with the trunk flexed and with the upper limbs alongside the chest; the second count was taken with the body extended and the upper limbs raised. In both cases the body and limbs were horizontal. The only important difference between both extreme positions of the limbs was the length of the arteries and, of course, their transverse diameter. In the flexed position the arteries were larger and a greater quantity of blood could pass through. On the contrary, when the body was extended the arterial tubes were of a smaller diameter and a smaller quantity of blood was allowed to pass through. As a result we always found that there was an increase in the pulse rate when the body was extended. This difference varied between two and four pulsations a minute. We consider this acceleration of the heart beat as a reaction against a sudden increase of resistance to the blood caused by the diminution in the diameter of the arteries. Besides, there is, of course, the possibility of an increased blood flow for a new redistribution. In our experiment when the arteria anonyma, left carotid and left subclavian become smaller tubes a smaller amount of blood will be admitted through and the surplus will be passed on through the arcus aortae and aorta descendens into other organs (abdominal). The instinctive forced extension which accompanies the yawn and generally all states of fatigue might be explained by this change in size of the arterial tubes, first of all the aorta[1].

We believe that the pericardium by pulling on the arcus aortae and the large arterial blood vessels plays a very important rôle as a mechanical device for the redistribution of blood between the head and upper limbs on the one hand and the abdominal organs and lower limbs on the other.

[1] Another study will follow in which we shall consider the aorta with all its large ramifications as an apparatus for the redistribution of blood under various circumstances.

V. THE PROTECTIVE ACTION OF THE PERICARDIUM AGAINST SYSTOLIC SHOCK

The force of blood thrust against arterial tubes during systole is quite important (48). The column of fluid pushes vigorously against an arched tube

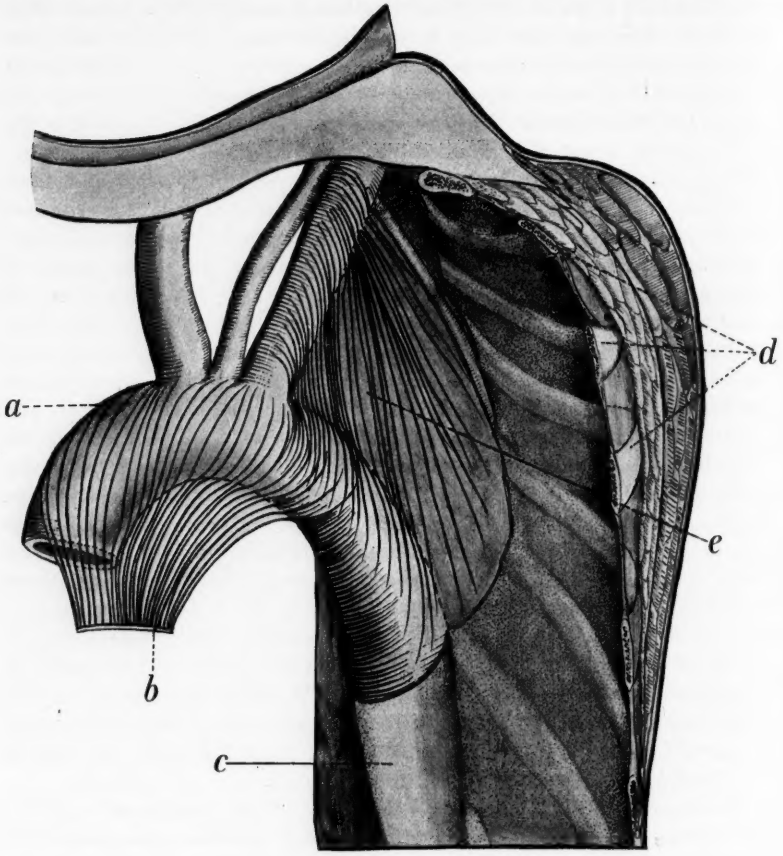

Fig. 14. Mechanostructures projected on large arteries of the heart. (Human.)
a, arcus aortae; *b*, fasciculus aortico-periatrialis; *c*, aorta thoracalis; *d*, costae; *e*, fibrae aortico-subclaviales.

(arcus aortae). Under such conditions there is a tendency for this arched tube to straighten out, and this situation, if it really occurred, would endanger the patency of openings in the arteria anonyma, left carotid and left subclavian. By the same mechanism and with the same results the distance between the left subclavian and aorta descendens tends to be increased. But, owing to the

fact that the pericardium is fixed to the arcus aortae, this arch remains almost fixed in its situation (fig. 14, fasciculus aortico-periatrialis). The aortic arch goes up and down as a unit and does not distend itself. The same effect upon the arcus aortae is produced also by the ligamentum cardio-aorticum (fig. 6). A similar rôle is probably played by the fibrae aortico-subclaviales (fig. 14) which are placed between the aorta descendens and the left subclavian artery.

VI. SOME COMPARATIVE DATA

As we have already seen, the erect attitude of the body and the close connection of the pericardium with the diaphragm cause the orientation of the majority of bundles of fibres of the pericardium. The association of effects upon the pericardium of hyperextension movements with deep inspiratory movements (rendered possible by the close connection of the diaphragm with the pericardium) resulted in the construction of a very strong and complex apparatus which is best shown in the human pericardium.

In animals with a horizontal position of the trunk and with no connections between the diaphragm and the pericardium this membrane is very thin and the orientation of fibre bundles is quite different. We examined the mechanostructures of the pericardium in two animals noted for their rapidity of movements: the dog and the horse.

(*a*) *Dog* (fig. 15)

In this animal the heart is suspended by the vena cava superior (with the vena azygos) and the vena cava inferior. Both veins show around them a thick layer of connective fibres which are orientated longitudinally (fasciculus cavo-diaphragmatis). Furthermore there is a strong ligament connecting the first rib with the vena cava superior (ligamentum cavo-costale). At the opposite pole there is a restricted connection between the diaphragm and pericardium (ligamentum phreno-apicale). These two ligaments present a resistant basis of suspension for the heart, and during inspiration the diaphragm pulls on the ligamentum phreno-apicale and gives rise to a certain extent to forces similar to those above described in Man. But these forces are far less powerful than those present in Man.

There are in the dog three ligaments connected to the sternum (ligamentum cavo-sternale, ligamentum phreno-sternale and ligamentum sterno-apicale). These ligaments seem to be quite lax in the opened thorax. The inspiratory movements are here very similar to those of an harmonium, the thorax being elongated cranialwards and caudalwards at the same time. Concomitantly the strong musculus triangularis sterni (in the dog it is very strong and large) approximates the costal cartilages and increases the sagittal diameter of the thorax. By these means the three ligaments are extended and their function is explained[1].

[1] The detailed explanations of the complex factors at work in this place will be presented in another work upon "Triangularis sterni and the mechanostructures of the anterior body wall."

(*b*) ***Horse*** **(fig. 16)**

The most impressive feature of the pericardium of the horse is its disproportionate thinness compared with the great mass of the heart. The pericardium in the horse is much thinner than the human pericardium. Its intimate structure and the orientation of its fibres are also very simple. Thin bundles, homogeneously placed throughout the pericardium, connect the large

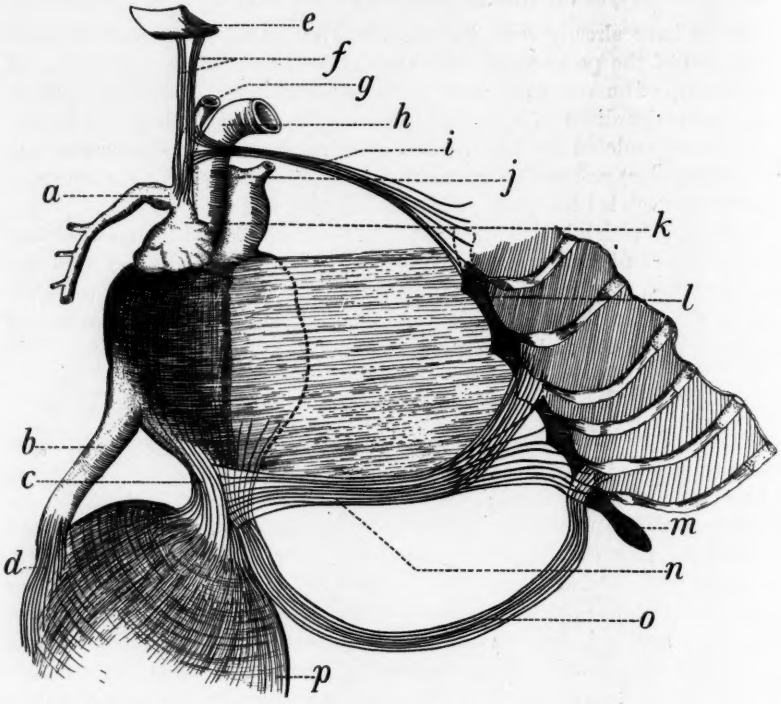

Fig. 15. Mechanostructures of pericardium. (Dog.)

a, vena azygos; *b*, vena cava; *c*, ligamentum phreno-apicale; *d*, fasciculus cavo-diaphragmatis; *e*, costa I; *f*, ligamentum cavo-costale; *g*, vena cava superior; *h*, arcus aortae; *i*, ligamentum cavo-sternale; *j*, arteria pulmonalis; *k*, auriculum dextrum; *l*, sternum; *m*, processus xiphoideus; *n*, ligamentum phreno-sternale; *o*, ligamentum sterno-apicale; *p*, diaphragma.

blood vessels with various portions of this membrane (fasciculi arterio-pericardiaci), and some stronger fasciculi pass from the superior vena cava to the posterior vena cava. But the strongest fasciculi are orientated in such a way that they suspend the heart and aorta descendens to the fascia of the prevertebral muscles (fasciculi aortico-prevertebrales).

The reason for this thin pericardium, which encloses a very big heart with strong power of contraction, is explained by the fact that this heart is not

supported by the pericardium itself but by the sternum. We must take into account also that the connections of the pericardium with the diaphragm are still looser in the horse than in the dog.

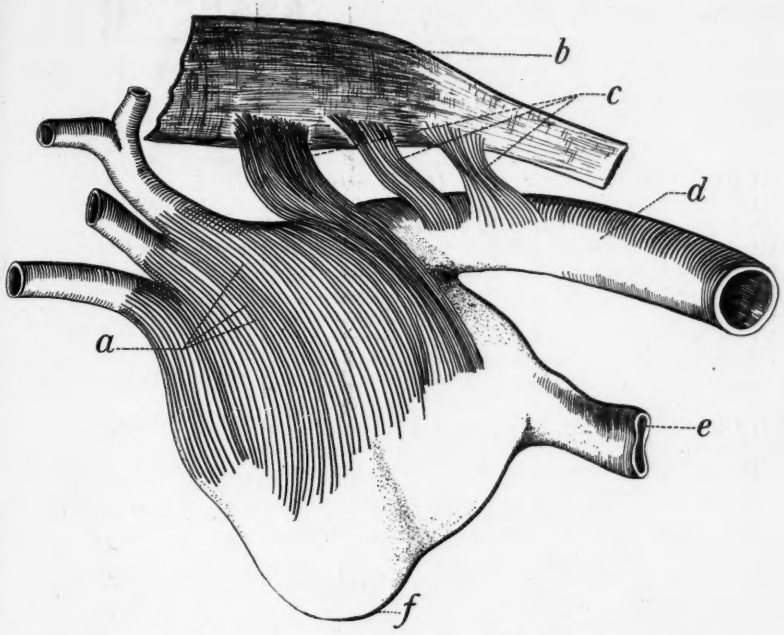

Fig. 16. Heart and vessels in horse. Some of the mechanostructures of pericardium projected. *a*, fasciculi arterio-pericardiaci; *b*, musculus prevertebralis; *c*, fasciculi aortico-prevertebrales; *d*, aorta descendens; *e*, vena cava inferior; *f*, apex.

VII. CONCLUSIONS

The pericardium shows a very definite orientation of fibres in its structure, determined by various mechanical factors: mostly forces of traction outside the pericardium and pressures inside the pericardium. All these forces are produced by some general functions of the body: respiratory movements and movements of the spinal column.

In the fundamental structure and orientation of fibres in the pericardium, its relations with the diaphragm, the attitude of the body and the type of respiration are of the greatest importance.

The posterior part of the pericardium must be considered as a reinforcement of the atrial walls and also as a fixation mechanism for the lung roots.

Considered as a unit the pericardium plays a very important rôle in the distribution and redistribution of blood volumes between certain large territories of the body.

By the arrangement of its insertion the pericardium protects the large blood vessels against systolic shock.

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ABDOMINAL PREGNANCY IN ANIMALS, WITH AN ACCOUNT OF A CASE OF MULTIPLE ECTOPIC GESTATION IN A RABBIT

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Abnormalities in the position of the developing embryo are by no means uncommon in the human subject, but are rare amongst other Mammals. The present account records the presence of four foetuses in the abdominal cavity of a tame rabbit. The doe was a black and white English rabbit born in January, 1930, and at the time of dissection was 1 year and 10 months old. She had bred three times, but each time only one young rabbit was born dead. No signs of ill health were noticed by the owner. The last birth was in February, 1931, when the mother produced one abnormally large dead foetus. She had been a successful foster mother to litters of four and two respectively. The brother of this doe is sterile; the parents were apparently normal.

The rabbit was one of twenty-five dissected by the elementary class. It was observed that the abdomen was enlarged, and a hard lump could be felt in the right inguinal region. The students who dissected the specimen were warned to look out for foetuses, but did not expect to find these in the abdominal cavity! On opening the cavity, two ovate tumour-like bodies became visible. The larger of these lay in the right posterior portion of the coelom, lateral to the bladder and vagina, and the smaller was situated under the left side of the arched diaphragm, pushing the stomach in a posterior direction and the liver over to the right. Each was held in place by from five to eight narrow strips of tissue, acting as anchoring processes and bearing small blood vessels. There was no marked vascularisation of either the "tumour" or its supports; both were pale in colour. The two bodies were removed and preserved for examination, and the students were supplied with another rabbit so that the reproductive organs might be left undisturbed. In addition to the two large bodies, three smaller structures were found floating freely in the coelom. These were also removed and preserved.

The rabbit was very fat but exhibited no signs of disease. The heart was rather large. The lungs were normal and no abnormalities were apparent in any of the endocrine glands. The ovaries were large, the right ovary measuring 13 × 7 mm. and the left 15 × 9 mm. The right ovary had two corpora lutea and two black swellings full of liquid, and the left ovary eight corpora lutea and four similar blackened vesicles. The funnel of the left Fallopian tube lay in its normal position, but on the right side the funnel was wholly anterior to its ovary. Both funnels were abnormally large, measuring 13 mm. in length on

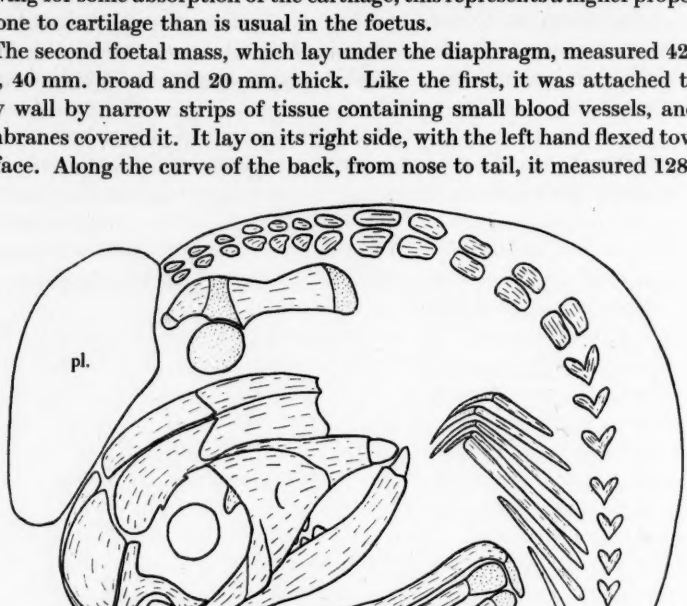
the right and 19 mm. on the left. The Fallopian tube was also of wide calibre, being at first 4 mm. in diameter and highly vascular. A seeker passed readily through the funnel into the tube, which enlarged to about 6 mm. diameter as it neared the uterus of its side. Both tubes showed undoubted signs of degeneration at this point, the walls becoming fatty, soft, and so thin-walled as to be transparent. The whole of the broad ligament was loaded with fat and it was difficult to isolate the tube, or to determine whether it had actually burst. The opening of the tube into the uterus, the uterus itself and its aperture to the vagina were normal on both sides. The peculiarities of the genital organs and their ducts were thus the large size of the ovaries, their blackened follicles, the enlargement of the funnels and Fallopian tubes, and the degeneration of the posterior portions of both tubes.

The five foetal remains were next examined. The largest, which lay in the right inguinal region, measured 55 mm. in length, 46 mm. in width and 32 mm. in thickness. It was fastened to the body wall by eight strips of connective tissue, whose small blood vessels were apparently in communication with the ilio-lumbar arteries and veins, but the vessels were so slight that it was difficult to determine this with accuracy. Two membranes covered the foetus, obviously the foetal chorion and amnion. There was no amniotic fluid. Within lay a fully formed mummified foetus, whose right side had been absorbed so that the skeleton was exposed, but whose left side still had flesh on it. The foetus was hard and stony, its bones were very well ossified, and as dark in colour as if stained with alizarin. It lay curled up, with the head close to the right side of the pelvis, and the right arm folded with the hand directed dorsalwards (see figure). The length from nose to tip of the tail along the curve of the back was 152 mm., which is the length of a full-term foetus of average size. The skull was almost completely ossified, and the incisor and premolar teeth were plainly visible. The eye had sunk in the orbit. The vertebral column, with well-ossified paired arches, showed through the membranes before the removal of the latter. Seven ribs, somewhat crushed, could be seen. Radius and ulna were separable. The left side of the foetus, which lay in contact with the dorsal abdominal wall, had undergone much less absorption than the right side. The bones were here covered with hard flesh, and the only parts of the skeleton visible on the surface were the left ilium and hind-limb and the toes of the left foot, which lay over the left side of the occiput. The much twisted umbilical cord was lying on the surface. The remnant of the placenta was of the usual flattened shape, and measured 23 mm. long, 19 mm. broad and 8 mm. thick. Only a small portion of it is seen in the figure as it curved round towards the left side of the foetus.

It is remarkable that although this foetus had had no separate existence, its bones were more completely ossified than in the early post-natal condition. For example, in a 2-day rabbit the scapula measured 18 mm. in length, but of this length 6 mm., or one-third, was cartilaginous suprascapula. The bony part was therefore 12 mm. long. In the mummified foetus the length is 17 mm., of which 15 mm. is bony and only 2 mm., or one-eighth, is cartilage. Even

allowing for some absorption of the cartilage, this represents a higher proportion of bone to cartilage than is usual in the foetus.

The second foetal mass, which lay under the diaphragm, measured 42 mm. long, 40 mm. broad and 20 mm. thick. Like the first, it was attached to the body wall by narrow strips of tissue containing small blood vessels, and the membranes covered it. It lay on its right side, with the left hand flexed towards the face. Along the curve of the back, from nose to tail, it measured 128 mm.



The largest foetal mass stripped of its membranes and dissected superficially to show the position of the parts of the body. All the bones figured could be seen through the remains of the skin, and the muscles of this side had almost entirely disappeared. The backbone is indicated by the neural arches in so far as these were exposed by maceration. Bone lined, cartilage dotted. *pl.* placenta. Drawn from a photograph. × 2 approx.

and was probably between 25 and 30 days old when it died. The maceration of this foetus was much less advanced than in that first described. The muscles and skin were comparatively soft, and even on the left exposed side a considerable amount of tissue had to be cleared away to show up the skeleton. As regards age, this foetus was younger than the former foetus. It was smaller, and there was a larger proportion of cartilage in its skeleton. Thus the scapula was 13 mm. long, 10 mm. was bony and 3 mm. cartilaginous, or approximately one-quarter of the length was cartilage. Compare these figures with those for

the first foetus. This specimen had no trace of a placenta, and the umbilical cord was not visible on the surface.

The three floating bodies, which were soft and not at all mummified, were about 20–25 mm. long, 20 mm. broad and less than 10 mm. thick. Two contained small foetuses about 10 mm. long, enclosed by their membranes and with their placentae. Although maceration had begun, it was still possible to trace the foetal form, to shell it out of its membranes and to determine its relationship to the placenta. Some ossification of the skeleton had occurred. The third body appeared to be a dermoid cyst. It contained three masses separated by fibrous tissue. Each contained calcareous concretions, which were effervescent in hydrochloric acid. There was no trace of a foetus or placenta, and this body differed from the others in being foetid.

HISTORY

Although ectopic pregnancy has been recorded many times in the human subject, very few authors have reported it in other Mammals, despite the large numbers of animals dissected. Thus, the Index Catalogue of the Library of the Surgeon-General's Office, United States Army, devotes over a hundred columns to lists of papers on the subject in human beings, and only half a column to its occurrence in animals. A study of the literature does not greatly augment this short list, and the records refer to a small number of species only, mostly domestic Mammals. There are records for the hare, rabbit, cow, ewe, sow, cat and bitch, mostly one for each species, except in the rabbit and hare. Those in the rabbit, it may be noted, are frequently in animals employed for experimental purposes.

The earliest account of ectopic pregnancy in animals is given by P. Rommel in a Physico-medical Discourse, published at Ulm in 1680, and refers to the hare. A very large hare was brought in by a huntsman, who found two large spheres in the abdomen close to the stomach, among the folds of the intestine. Rommel made an incision through the membranes surrounding one of these growths and found in it a compact hairy mass, which he thought at first was similar to the hair balls found in the stomachs of goats, oxen and horses. But further investigation disclosed a perfect little hare. He says that he believes this hare developed outside the uterus and near the stomach, as was described by the huntsman. He then proceeds to discuss a number of cases of conception in cavities of the body other than the uterus (stomach, intestine, scrotum, Fallopian tube, etc.), nearly all of which are incredible, and concludes that it is not impossible that his little hare may have been conceived outside the uterus, and compares this phenomenon with the presence of parasites in various parts of the body. He states that several anatomists have testified to the occurrence of tubal pregnancies[1], and adds that as it is now held that conception in the first place is in the tube, this is not extraordinary. Indeed a foetus

[1] Presumably in Man as no animal is mentioned.

has been seen attached to the outside of the tube and consequently conceptions must be possible in cavities of the body other than the cavities of the generative ducts.

In 1685 Buissiere, after describing a case of retention of the foetus after ectopic pregnancy in a woman, adds an account of a similar occurrence in a hare. Like Rommel's specimen, the animal was brought to Buissiere by huntsmen, who had found numerous young in the abdomen. Buissiere examined the specimen and described the young, still within their membranes, lying in the coelom and having no other connection with the uterus than the placental attachment. He did not, however, mention any rupture of the uterus, and it is not clear if the foetuses were actually attached when he saw them.

It is not surprising that vague and fantastic theories were built around such rare and monstrous foetations. Some refused to believe in them and scoffed at them as miracles; others accepted and attempted to explain them, claiming, as Rommel did, that gestation could occur in parts of the body other than the generative organs. Even as late as the early nineteenth century, when the subject was again brought to the notice of the medical and anatomical world by records in human beings and animals, it was believed that the foetus could implant itself on the abdominal wall by means of a placenta, and develop normally in that position. Several records in the ewe (Simonds) and the hare (Dohrn, Dartigolle) were described, and at the end of the century cases were discussed in the medical societies of London and Berlin, and raised the whole question of abnormal pregnancy in Man and animals, with the result that many of the old errors were swept away, and the ground cleared for a more adequate explanation of the abnormalities recorded. It is unfortunate that most of the accounts relating to animals during the period 1890 to 1910 are in medical journals, where the zoologist is not likely to meet with them.

In 1898 Drs Pembrey and Bellingham Smith exhibited at a meeting of the Obstetrical Society in London five foetal sacs found free in the abdominal cavity of a rabbit kept for experimental purposes. Four of the sacs contained a full-term foetus, the fifth carried four full-term young. A more detailed account in 1904 described the case as one of multiple utero-abdominal pregnancy, on the evidence that "the uterus showed evidence of a former rupture in the shape of an old scar at the junction of the two uterine horns." To the comparative anatomist it is clear that these authors are confusing the vagina of the rabbit with the uterus of the human female, for the uterus of the rabbit is paired, not median. The case appears to be one of ruptured vagina at parturition, probably owing to the quadruple gestation sac described above. This interpretation receives confirmation from the equality in age, and freedom from attachment of the foetal sacs. Sir John Bland Sutton, however, in his Purvis Oration for 1904, makes Pembrey and Smith's case the main support for his thesis that all apparent abdominal pregnancies are secondary, having burst out from either the Fallopian tube or the uterus into the coelom. In the

human subject tubal pregnancy is the common cause of the extrusion and in other Mammals a ruptured uterus.

In Germany, at the beginning of the twentieth century, several ectopic pregnancies were described in animals, and aroused such interest that an attempt was made to bring about the condition experimentally. Wolff (1902) claimed to have found primary abdominal pregnancy in a rabbit, whose single full-term foetus was attached by a vascular network to the spleen and stomach. Former abdominal foetuses had been found free in the abdomen, and because this foetus was fixed, he regarded it as a true case of abdominal placentation. But his specimen was a rabbit which had been operated on some time before the finding of the foetus. A piece had actually been removed from the uterine wall for experimental purposes. The case has therefore all the symptoms of artificial utero-abdominal pregnancy. Another account of supposed primary abdominal placentation was published in a German Gynaecological Journal by Kamann in 1903. The specimen was also a rabbit, and contained one foetus attached to the omentum by a pedicle. But re-examination of the specimen showed that this case, like the preceding one, was due to a ruptured uterus and extrusion of the foetus, for the uterus exhibited the scar of a former rupture. Later, Kamann withdrew his original explanation, and substituted for it: "Apparent abdominal gestation in the rabbit, after primary uterus rupture." A third example in the rabbit occurred in a specimen used for experiment, and this was described by Henneberg (1903) and Happe (1903). The right uterus had been ligatured 3 days after copulation, and 8 days subsequently the animal was killed. Autopsy revealed four normal foetuses developing in the right uterus. On the left side there was an open fistula and beyond it one normal foetus *in utero*. The number of fresh corpora lutea corresponded to the number of young in the uteri. But lying in the body cavity were three dead foetuses from 6 to 9 cm. long, enclosed in a single membrane and attached by bands to the wall. These obviously belonged to an earlier gestation, and the ruptured left uterus suggested that they had reached the coelom through the fistula. The authors did not attempt to explain how the foetus developing in the uterus had managed to dodge the opening of the fistula during its passage along the uterus, nor why the rupture had remained unhealed. The most interesting case was an experimental one in the rabbit, described by Sittner in 1903. He took a rabbit which was 8 days' pregnant, opened one uterus by making a slit 1 cm. long, and hooked out into the abdomen a foetal sac 7·5 mm. in length. The uterus was then sewn up, and gestation proceeded normally. After 33 days two normal living young were born. The rabbit was then killed, and dissection revealed four foetuses in the coelomic cavity. One of these had attached itself to the body wall. Its old placenta was free, and the anchoring strands represented new tissue. Sittner thought that this was a case of secondary abdominal pregnancy, as it undoubtedly was. He suggested that three of the foetuses escaped through the funnel of the Fallopian tube into the coelom by an anti-peristaltic action of the uterus.

DISCUSSION

Five explanations have been given by authors to account for the presence of foetuses in the abdomen of a living animal. These are:

(1) Genuine abdominal pregnancy, by the formation of a placenta on the peritoneal lining. This is an old view, and was held before the process of conception was understood.

(2) Ovarian pregnancy, in which the egg is presumably fertilised before leaving the ovary, and develops there. Many human ectopic pregnancies have been thus described.

(3) Tubal pregnancy, resulting in rupture into the abdominal cavity. Here the fertile egg forms a placenta on the wall of the Fallopian tube or funnel, instead of on the wall of the uterus. The tube has limited powers of expansion and bursts sooner or later, expelling the foetus. The latter may retain its membranes, and may remain attached to the wall of the tube by its placenta and cord. If so, it will go on developing in the abdominal cavity and will make abdominal connections of a secondary nature. If, on the other hand, the placenta breaks away at the time of rupture, the foetus will die in the abdomen owing to the cessation of its nutritive supply, and will float freely in the cavity. The cause of the primary tubal attachment is not known. In animals producing many young at a birth, the uterus may be already fully occupied when the last fertile egg comes down. This does not apply, however, to the human subject, where tubal pregnancy is the most common abnormality of placentation. Retention of the dead foetus is always associated with absorption of its soft parts, and mummified foetuses have been found more than 20 years after gestation in women.

(4) Normal uterine pregnancy resulting in rupture before parturition. This occurs in animals only, and may be brought about by twin, triple and quadruple gestation, where several foetuses within one set of membranes occupy the uterus in a region adapted for bearing one. The strain on the uterine wall may result in its rupture with results as in (3) above.

(5) Normal uterine gestation, with anti-peristaltic uterine contractions of sufficient strength to drive the foetus backwards along the tube and through the funnel into the abdominal cavity. This is merely a theory and has no evidence in support of it.

Of the five interpretations which have been suggested to explain abdominal foetation, there are no authentic cases of (1) and (2), and no evidence is available for (5). Supposed cases of abdominal placentation have proved to be secondary in nature, and supposed ovarian pregnancy is usually tubal, with subsequent attachment close to the ovary. Doran, who had seen many specimens of abdominal foetuses, wrote as long ago as 1893: "When some observer can demonstrate to us a specimen where a foetus as minute as that which I now

exhibit[1], but recent and entire, is to be seen lodged in a true gestation sac inside the ovary or on the peritoneum away from the tube, then we shall begin to believe in primary ovarian and abdominal gestation." The third and fourth explanations, i.e. ruptured tubal or uterine pregnancies, are the only ones for which there is direct evidence. In the human subject the tubal type is not uncommon, and Tait (1892) described a case in which the foetus burst the tube at 10 weeks, as evidenced by the mother's symptoms, but retained its connection with the tubal placenta so that it was able to continue its development in the coelom. A ruptured uterus in woman does not allow of abdominal development, because the haemorrhage following the rupture is fatal to the mother. Hence human cases of abdominal development are of necessity tubal in origin. In animals, on the other hand, the cases recorded previously have all been utero-abdominal in nature.

The present case differs from all the earlier ones in two particulars. Firstly the evidence points to tubal pregnancy in an animal. This is suggested by the enlargement and rich vascularisation of the Fallopian tubes, the fatty degeneration of their posterior portions and the absence of any scar on the uteri. The fact that there is no trace of placental tissue on the inner wall of the tubes is no evidence against this view, since the last pregnancy occurred 9 months previously and placental tissue is readily absorbed. Secondly the dead foetuses are of different ages and exhibit varying degrees of maceration. This suggests that they belong to separate pregnancies, and this is the first case in which repeated abdominal foetation has been recorded in an animal. The two smallest foetuses are about the same age. Each is approximately 10 mm. in length and has its own placenta. These two probably broke away together from the maternal tissues at an age of about 12 days, and died in the abdominal cavity owing to the stoppage of their food supply. The softness of the foetal sacs and the very slight degree of absorption point to a recent rupture. The two large foetuses have undergone about 25 days and full-term development respectively. This can be deduced from their size and the degree of ossification of their bones. The largest foetus evidently lived in the abdomen beyond the full term of 30 days. In size, even in its mummified and partially resorbed state, it is as large as a new-born rabbit. Its bones, however, are older than this, as ossification has proceeded well beyond the parturition period (see p. 109). The marked difference in the absorption of the soft parts indicates that these two large foetuses belong to two gestation periods, so that three such periods are represented by the four foetuses. Whether these three correspond to the three known pregnancies of the animal we cannot now determine, but as there were only three pregnancies, it seems likely that each produced one stillbirth (see p. 108) and one or more abdominal foetuses. There is apparently nothing to account for the abnormal foetation. The stillborn young found the right way out through the uteri and vagina, so that closed ducts were not the cause. Dissection also showed that these were normal and patent. There was no record

[1] One inch in length.

of ill health, of over-production of young, or of more than one young in a single set of membranes stretching the ducts unduly. The stillborn young were presumably uterine gestations. Did the presence of dead foetuses in the abdominal cavity cause their death? Were the tubes originally too wide, so that the fertile eggs settled down prematurely there? Or did the luteal and pituitary hormones act too rapidly, stimulating attachment before the uteri were reached, thereby widening normally slender tubes? Nothing in the specimen gives any clue to the answers to these queries.

The two youngest foetuses formed no abdominal attachments, and from this it can be inferred that the placental connection severed itself at the same time as the tubal break, so that the little rabbits died there and then. The two large foetuses, however, were anchored by strips of living tissue to the abdominal wall. This implies that they lived for some time after extrusion from the tubes, and as a consequence must have remained attached by their placentae and umbilical cords to the tubes. From their position it is almost certain that they came from different tubes. The anchoring tissue was probably formed before they died. Death resulted from their inability to find the correct way to the outside world, and not from an interruption of their nutritive supply from the mother.

SUMMARY

An English doe rabbit, which had borne three dead young at different times, was found on dissection to contain the macerated remains of four foetuses in the coelom.

Two foetuses had died at about 12 days, and with their membranes and placentae, floated freely in the coelom. Two were attached to the abdominal wall by secondary anchoring processes.

The condition of the Fallopian tubes suggested that the four foetuses were *tubal* pregnancies which had burst out into the coelom. Two had broken away completely, and two had retained their placental connections up to 25 days and beyond full term respectively.

The chief points of interest in this case are that both tubal and uterine pregnancy had occurred, and that foetuses of three stages of development were present in the abdomen at the same time. This is the first record of tubal pregnancy in an animal, and of repeated extrusion of foetuses into the abdominal cavity.

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Note. The author has not seen the papers by Dohrn and Simonds. After the manuscript of the above was submitted for publication, a paper on Abdominal Pregnancy in a Cat, by Dr R. H. Hunter, appeared in *J. Anat.* vol. LXVI, No. 2, pp. 261–3.

ROENTGENOGRAPHIC OBSERVATIONS OF THE TIMES OF APPEARANCE OF EPIPHYSES AND THEIR FUSION WITH THE DIAPHYSES[1]

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A perusal of the various anatomical authorities shows considerable discrepancy regarding the ages at which the various epiphyses appear and fuse with their respective diaphyses. In former years, the only method of examination of epiphyses was to study the dead subject, but opportunities of doing this on an extensive scale are very rare, and in any case it is not always a simple process to determine from dried skeletons whether an epiphysis has been present or not. Moreover, with the exception of a study by Stevenson on a rather limited number of dried skeletons, no such attempt appears to have been made. However, it is by means of a roentgenographic examination that not only are the epiphyses more clearly and more certainly demonstrable in most cases in the living subject, but a larger series, with exact information concerning the respective ages, can be more easily studied and compared.

It has been felt that a much more accurate and authoritative account of the dates of appearance and fusion of epiphyses than is at present available would be of very great value for comparative purposes, especially in investigations concerning racial differences, effect of environment and climate, and for clinical and medico-legal purposes. It is hoped that this may stimulate further research in various directions, and such research will have a value in direct proportion to the accuracy with which the observations are recorded. The author can nowhere find accurate statistics actually based on the number of subjects examined with the exceptions of Galstaun, Sidhom and Derry and Pryor.

Galstaun presented the results of investigation of about 100 Hindu and Anglo-Indian girls aged 13 to 19 years, the work being limited to the regions of the elbow, wrist and hand. His figures have been made use of for the purpose of comparison, but these show no very gross disparity with the series presented here.

Sidhom and Derry investigated the union of some of the epiphyses of the upper limb in over 400 Egyptian boys, mostly between the ages of 14 and 20, being like Pryor particularly accurate in recording the ages. The boys were specially examined for the purpose of their research. As compared with the

[1] Read at a meeting of the Radiological Section of the Victoria Branch of the British Medical Association, 12 May, 1931.

boys in the Australian series, the majority were fused at the same age in the cases of the medial epicondyle and both extremities of the radius, a year earlier for the lower conjoint epiphysis of the humerus, distal epiphysis of the ulna and for the first metacarpal, and two years earlier for the distal phalanx of the thumb. With regard to the extremes, there were instances of both earlier and later fusions in the Egyptian series.

The work of Pryor, however, is of monumental importance, for, as the result of a study of 554 roentgenographs of the hands of children from 3 months to 14 years of age, he came to the following conclusion: "The bones of the female ossify in advance of the male. This is measured at first by days, then months, then years," a conclusion which is abundantly confirmed elsewhere. Moreover, he has carried his research further and studied the roentgenographs of 140 foetuses from $10\frac{1}{2}$ to 38 weeks of age, 71 being male and 69 female, and reached the very unexpected result that "in the ossification of the human skeleton, the female is in advance of the male from the earliest developments of centres of ossification in the embryo and throughout intrauterine life, progressing from days to weeks and months." Such advance apparently takes place even before external sex differentiation can be determined.

Although abundant evidence of the advance in females is present from the period about birth, Pryor does not give any data regarding such priority from the "earliest developments of centres of ossification."

Stevenson studied the periods of fusion only in 110 skeletons aged between 15 and 28, including 83 from 15 to 25 years of age. He makes the following extraordinary criticism of the X-ray examination, which is quite unjustified: "The recent assertion by Pryor, made without any confirmatory evidence, that the epiphyses in the female unite 3 to 4 years earlier than in the male receive no support in this work. On the contrary, the reader is warned against relying too confidently upon the apparent condition of union or of non-union in the radiogram which is merely a confusing medley of shadows."

However, as Stevenson has not separated the skeletons of the females from the males, they are not of value for the purpose of comparison with the Australian series, and in any case, of the 110 subjects between 15 and 28, but 20 are female, of whom 18 are between the ages of 15 and 25. Many of the conclusions arrived at can readily be challenged, particularly the alleged constancy of behaviour of the epiphyses with regard to the ages of fusion.

Borovansky and Hnevkovsky investigated the bones of both the upper and lower extremities of 352 boys of all ages up to 19 years, the roentgenographs being specially made for the purpose of the research. Even with this limited material, all of boys from Prague, charts representing the periods of ossification are shown, although the actual number at each age is not given. The work, however, is valuable, inasmuch as many measurements of the size of the various epiphyses at different ages are given.

Recently Paterson has investigated about 1000 films and roughly tabulated his results, although he gives no actual statistical figures.

Davies and Parsons have described the appearances of epiphyses as seen in roentgenographs, giving detailed information of the ages when these were seen, but no numerical data from which the relative frequency can be ascertained are given. Unfortunately, the sexes of the individual examples are more frequently omitted than inserted in the text.

The subjects of this examination were mostly hospital patients, practically all of whom are of European descent, and as nutritional diseases, such as rickets, scurvy, etc., are rarely met with in Australia, the error from including such possible conditions is practically insignificant. To avoid duplicating details of the same subjects, and to assist in checking off age and sex particulars, the names of the individuals and serial numbers of the films were also recorded. Notes were made only of such epiphyses whose presence or absence could be definitely established. All others are excluded from the records.

The ideal method of presenting the results of such an enquiry would be by means of graphs, but the material available is not nearly sufficient for the purpose, although Stevenson prepared graphs for a very much smaller series. To give percentages, even roughly, where in no instance are there 100 subjects in any age group is likewise objectionable, although other authors, notably Paterson, have done so. Many such percentage computations must be sheer guess-work, and appear to have been made even when less than a dozen subjects were in question. The only honest, and, it is thought, the best method is to give the actual figures in each age group, and this has been done.

Stevenson and Paterson have both summarised in considerable detail the ages of appearance and fusion of the different epiphyses as given by numerous authors. Although this is very useful as serving to demonstrate the various discrepancies, a repetition of such lists here would serve no useful purpose, and it would be better to discard all data except those based on actual statistics.

With regard to the various descriptions which follow, the following points were specially noted with reference to each sex:

(*a*) Youngest subject where epiphyses in question were found to be present.

(*b*) Ages at which the majority of the epiphyses in question were present.

(*c*) Oldest subject in whom epiphyses had not yet appeared.

(*d*) Youngest subject where epiphyses were found to be fused with the diaphyses.

(*e*) Ages at which the majority of the epiphyses were found fused.

(*f*) Oldest subject in whom epiphyses had not yet fused.

Though classifications have been made regarding the sex, and notes have likewise been taken with respect to the sides, whether right or left, any classification regarding the side would considerably burden this article, but as yet, no detailed study has been made concerning the possibility of any appreciable difference of one side as compared with the other. Moreover, it is doubtful whether such a difference exists, although in right-handed individuals it is quite conceivable that the different function of one side as compared with the other might lead to some variation of the times of appearance of epiphyses.

It has been noticed repeatedly that an epiphyseal centre is present on one side although absent on the other in the corresponding bone of the same individual. Of 25 such examples in different bones, the epiphyses were noted 16 times to be present on the right side but not on the left, whilst in the other 9 they were present on the left but not on the right.

Koehler has stated that the order of appearance of epiphyses is not necessarily the same on both sides, even in the same individual, as may be noted in the example of the carpal bones of a child given later (see fig. 2). This does not accord with Pryor's observations, "Regardless of the variations (normal) the ossification is bilaterally symmetrical." Nor are they necessarily the same in twins, as shown by Borovansky and Hnevkovsky, who figure the hands of twin boys aged 6, where in one boy the navicular was present on one side but not on the other, and was absent on both sides in the brother. In the first boy the multangulum minus was present on both sides, but absent on both sides in the brother.

With regard to the time of fusion, that this process usually occupies only a few months seems to be indicated by an observation of the epiphyseal plate between the tip of the olecranon process and the diaphysis of the ulna in a subject aged 15 which showed as a considerable gap on the roentgenograph at 16 December, but at 29 May next not the slightest trace of the epiphyseal line could be detected. The author believes that Galstaun's classification into "commencing union," "earlier stage of same process," "nearly complete union" and "union just complete" is superfluous and unnecessarily complicates the observations. The author has merely noted non-fusion or fusion, the latter referring to entire disappearance of the epiphyseal plate, which is in most cases not difficult to determine. A linear shadow which may sometimes persist even for years at the junction of epiphysis and diaphysis is interpreted as fusion. When comparing Galstaun's records, his classification "union just complete" is included with fusion, the others as non-fusion. Stevenson, as well as Sidhom and Derry, have likewise described several stages of fusion.

The study of primary centres and epiphyses during intra-uterine life has been dealt with in another article.

THE CLAVICLE

The medial extremity of the clavicle was noted in 655 instances under the age of 30. The youngest female in whom an epiphysis was noted was aged 11, where it was present on the right side but absent on the left, and the youngest male 12, the oldest being 25 years of age in a male and 26 years and 11 months in a female in whom it was present on the left but absent on the right, in each case being present on both sides. The centres are infrequently seen under 17 or over 22 years of age. Stevenson states that it may be delayed until 28 years, but of 33 subjects aged 27 to 29, no epiphyses were seen. At no age do more than 64 per cent. of clavicles appear to be possessed with epiphyses, suggesting the possibility that the epiphyseal centre for this bone is not a

constant feature, but it must be remembered that such centres are frequently very difficult to demonstrate, partly owing to the irregularity of the sternal end of the clavicle, as well as to a mixed background of intrathoracic structures, vertebrae and posterior parts of ribs, whilst confusion with costo-transverse and costo-central articulations must be particularly avoided.

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
11	12	2	1	0
12	11	9	0	1
13	3	15	0	0
14	8	10	2	2
15	10	11	2	1
16	16	14	4	1
17	12	12	5	5
18	10	15	2	3
19	25	11	11	7
20	28	19	12	7
21	14	20	7	11
22	18	11	5	4
23	17	16	4	4
24	18	15	4	1
25	19	18	2	2
26	10	8	1	0

From the above table it appears that the majority of young people of both sexes aged 21 possess epiphyses for the sternal end of the clavicle, but at all other ages the majority show absence of epiphyses. This suggests that in the majority of instances the centre appears at the age of 21 in both sexes, and that fusion takes place in the majority of instances at the age of 22 in each sex.

INFERIOR ANGLE OF THE SCAPULA

The epiphysis for the inferior angle of the scapula was clearly demonstrated in one subject only, a female aged 17, where the scapulae were thrown clear of the bony chest, and where it was present on both sides. This centre is evidently but rarely seen, probably because the angle of the scapula is usually much obscured by the background formed by the various structures of the chest.

CORACOID PROCESS

The cartilaginous junction of the coracoid process with the body of the scapula was specially noted in three girls between the ages of $4\frac{1}{2}$ and $7\frac{1}{2}$ inclusive, when the arm was elevated above the horizontal. It was likewise seen in a boy aged 10 years and 3 months. Regular observations, however, of this process are rendered difficult by the overshadowing of the coracoid by the spine of the scapula as well as by the clavicle and head of the humerus in the ordinary position of the shoulder with the arm adducted to the side, so that detailed classification could not be attempted.

EPIPHYSIS AT ANGLE OF CORACOID PROCESS

This epiphysis is usually present at the junction of the ascending and horizontal rami on the medial aspect, where it forms a thin scale of bone (see fig. 1).

The youngest instance where this was noted was a girl aged 10 years and

2 months, where it was present on the right side but absent on the left. This was the only epiphysis out of 54 instances in both sexes aged 10 to 12, but examples were noted in a girl aged 13 years and 10 months on both sides and in a boy at the age of 14. Of 240 instances (including 124 males and 110 females) aged 13 to 19 there were only 7 (6·36 per cent.) in the female although there were 23 (18·54 per cent.) in the male, suggesting a probability of greater frequency in the latter. In any case the rarity of these centres makes

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
13	6	18	2	0
14	10	16	1	2
15	6	13	1	2
16	23	14	2	5
17	25	14	1	5
18	9	25	0	8
19	31	24	0	1

it reasonably certain that this epiphysis is not a constant feature in the human subject. It would appear that in the female the appearance as well as the fusion with the ramus is earlier than in the male; thus of 40 females aged 18 and 19, no epiphysis was seen, although 9 such were present in 49 males of the same age. The epiphysis was most frequently found in males at the age of 16 and 17. The oldest female with unfused epiphysis was aged 16, where it was present on both sides, and the oldest male 19.

TIP OF CORACOID PROCESS

In boys aged 14 years and 7 months and 15 years and 6 months respectively (see fig. 1) not only were the usual centres present for the acromion and for the angle of the coracoid, but there were additional centres for the tip of the coracoid. In another boy aged 16 a similar centre for the tip of the coracoid was present as well as additional centres for the acromion process, although that for the angle of the coracoid was absent.

THE ACROMIAL EPIPHYSIS

The centre for the distal extremity of the acromion process sometimes consists of two or more fragments and is often seen in the same roentgenograph showing the presence of the epiphysis for the angle of the coracoid (see fig. 1). For clear demonstration, the roentgenograph should not be over-exposed:

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
13	6	7	2	0
14	4	10	4	4
15	4	9	2	5
16	7	10	4	8
17	9	5	0	2
18	6	14	0	6
19	10	19	0	2

very many views of the shoulder joint, even when clearly defining the various details of the joint itself, had to be discarded because of obliteration of detail of the acromion process resulting in a much smaller series than in the case of the coracoid process for instance.

The earliest appearances were in a girl on each side at the age of 13 years and 10 months, and in a boy at the age of 14 years and 11 months. It was present in the majority of females at the age of 14 and of males at the age of 15 years, and was fused in all instances in females at the age of 17 and in the majority of the males at the age of 17. Whilst the oldest female with an epiphysis was aged 16 years and 1 month, the oldest male was 19 years and 2 months.

Again, it is by no means certain that a centre always appears at the distal end of the acromion, for in 126 instances aged 13 to 19 (including 74 males and 46 females) there were but 41 (32·5 per cent.) epiphyses (inclusive of 27 males and 11 females) noted.

EPIPHYSIS FOR HEAD OF HUMERUS

At birth, the upper end of the humerus in the antero-posterior view appears to present two inclined planes meeting at a point in the centre. Over the medial of these inclined planes, the centre for the head of the bone makes its appearance during the first year after birth.

Of 25 instances in babes during their first year, the oldest without epiphyseal centre was a boy aged 6 months. The earliest centres noted were 4 months in the male and 5 months in the female. Davies and Parsons have seen it present in 2 of 4 subjects at birth. These are all earlier than any of the ages usually quoted.

Although Spencer was able to find by dissection in 40 foetuses weighing 7 lb. or more only nine instances of centres (22 per cent.) for the head of humerus, the author found this centre present in 6 of 10 foetuses over 294 mm. in length (including a female of 294 mm. and a male of 295 mm.).

GREATER TUBERCLE OF THE HUMERUS

Many radiologists, notably Cohn, doubt the existence of a separate centre of ossification for the greater tubercle, and are of opinion that this process is developed from extension of the centre for the head over the lateral aspect of the upper end of the diaphysis, but in numerous instances in young children, each centre has been noted side by side, one for the head lying on the inclined plane on the medial aspect and the other on the inclined plane on the lateral side. Unfortunately, in very many instances, the head of the humerus is obscured by the overhanging acromion process or even by the coracoid, so that it is frequently difficult to define the centre for the greater tubercle and to separate it from that for the head proper. Borovansky and Hnevkovsky give very good diagrams illustrating the appearances of the head and greater tubercle in the boys of Prague of various ages from 4 years and 1 month to 14 years and 7 months.

However, during the first year after birth, the earliest epiphysis for the greater tubercle was noted at 9 months (sex unknown), and 11 months in both sexes. Davies and Parsons report its presence in an infant aged 8 months. Its

absence was also noted at 11 months in a female and 3 years and 6 months in a male (both sides), while it was present in all five instances in females aged

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
Under 1	3	7	2	1
Over 1	1	14	1	3
2	5	4	5	2
3	8	6	6	4
4	7	5	3	4
5	7	7	2	1
6	13	4	3	2
7	7	7	0	0
8	1	7	0	0
9	3	9	0	1

2 years. Paterson reports the appearance of this centre at the end of the second or beginning of the third year, practically a year later than the author's observations seem to show. All other anatomists give 2 to 3 years.

FUSION OF CENTRES FOR GREATER TUBERCLE AND HEAD OF HUMERUS

After the first two years or earlier, the centre for the tubercle overlaps that for the head of the bone, the two fusing together, the line of union forming the anatomical neck (see fig. 1). The plane of fusion is very oblique and in very many instances, from the appearance of the roentgenograph even by stereoscopic examination, it is impossible to be certain whether fusion has occurred or not. From the above table it will be noted that fusion had taken place in half of the instances in girls at the age of 4 and in the majority of boys at the age of 5, although isolated instances of non-fusion were noted in a girl aged 6 (both sides) and in a boy aged 9. Davies and Parsons found non-fusion at the age of 12 in one instance.

LESSER TUBERCLE OF HUMERUS

Like other radiologists, the author has failed to find a specimen showing the presence of this centre and accordingly must doubt its existence. However, the position of the lesser tubercle in front of the bone would certainly make such a centre, if it were present, much more difficult to demonstrate, especially as it is usually impossible to secure a good lateral view of this part of the limb. Practically all anatomists describe its presence.

FUSION OF THE UPPER CONJOINT EPIPHYSIS WITH THE DIAPHYSIS OF THE HUMERUS

Age	No. of instances in girls	No. of instances in boys	No. fused in girls	No. of centres fused in boys
16	8	15	3	1
17	16	10	15	2
18	7	12	6	4
19	20	19	20	16

From the above figures it seems that the age of fusion of the combined epiphysis for the head and greater tubercle with the diaphysis seems fairly constant. The earliest fusion was at the age of 16 years and 8 months on both sides in a female, and 16 in a boy, the latest 18 in a female and 19 years and 2 months in the male. In none of 20 subjects aged 15 (16 boys and 4 girls) were these epiphyses fused, nor were any epiphyses noted in 30 others (including 14 males and 11 females) aged 20. The majority were fused at the age of 17 in females and 19 in males. Union was constantly found at 19 in females and 20 in males, which does not at all correspond to the various ages, 20 to 25 given by numerous anatomists, and they differ from those given by Paterson, namely 18 for females and 21 for males.

EPIPHYSIS FOR THE LATERAL EPICONDYLE

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
9	6	11	2	0
10	6	18	2	3
11	6	10	5	3
12	1	23	1	15
13	5	15	2	12
14	4	14	1	10
15	7	12	0	8
16	6	10	2	1

From the above table it can be noted that the earliest centres observed for this epiphysis were in a girl aged 9 (both sides) and a boy aged 10 years and 7 months. At the age of 11 in females and 12 in males, this epiphysis was found present in the majority of instances, whilst the oldest subjects with unfused epiphyses were aged 16 in each sex (both sides in a female). Despite the opinions of Cohn and Paterson, this epiphysis is probably present, like those of the capitulum, trochlea and medial epicondyle in every case at some period between 8 and 17 years. It was present in 37 of 52 males (71 per cent.) aged 12 to 14 and 22 of 29 males (75 per cent.) aged 13 and 14. The case figured by Paterson, which is described as an extension of the capitular epiphysis and which is stated to occur in 30 per cent. of cases, is certainly a fusion of the capitulum with the lateral epicondyle, which always takes place before union of the conjoint epiphysis with the diaphysis.

CAPITULUM

With the exception of male infants aged 1 week and 1 and 6 months respectively, where the capitulum was not present in any case, no babe under the age of 9 months was examined. The centre was present in the female child of 9 months on both sides and in a male aged 11 months, as well as in all older children. The author has found the capitulum present in every one of 21 instances at the age of 1 year, in all of 28 aged 2 and 20 aged 3. Davies and Parsons report its absence in one instance at 18 months.

THE TROCHLEAR EPIPHYSIS

Age	No. of instances in girls	No. of instances in boys	No. of centres in girls	No. of centres in boys
8	12	16	4	3
9	6	11	5	2
10	7	17	5	9
11	6	11	5	8
12	2	23	2	21
13	5	16	2	13
14	4	17	1	14
15	7	14	0	11
16	4	9	2	1

The earliest centres for the trochlea were noted at the age of 8 years and 5 months (both sides) in a girl and 8 years and 9 months (both sides) in a boy, whilst the majority of girls aged 9 and of boys aged 10 showed the presence of this centre. The epiphyses were still evident in a girl aged 16 on both sides as well as in a boy of the same age.

UNION OF EPIPHYSES OF LATERAL EPICONDYLE, CAPITULUM AND TROCHLEA

Many anatomical authorities describe the union of the epiphyses of the lateral epicondyle and trochlea on each side of the capitulum forming a new conjoint epiphysis which fuses at a later date with the diaphysis. From a roentgenological point of view this appears to be correct, and there is no valid reason for the supposition as suggested by Paterson, that in some 30 per cent. of cases the lateral epicondyle is formed by extension from the capitulum. If this were the case, one would expect to find intermediate stages

	Lateral epicondyle, capitular and trochlear epiphyses present		No. fused with each other	
Age	Girls	Boys	Girls	Boys
8	1	0	0	0
9	2	0	0	0
10	1	2	1	0
11	5	3	1	0
12	1	15	0	2
13	2	11	1	4
14	1	9	0	7
15	0	9	0	5
16	2	1	0	1

of this extension, such as may be observed in the case of the spinous process developed from the primary centre of the scapula, or the main part of the olecranon process from the shaft of the ulna, but such intermediate stages are not seen. On the contrary, the adjacent margins of the epiphyses for the lateral epicondyle and capitulum prior to fusion are always smooth and well defined.

The union of the lateral epicondyle and trochlea on each side of the capitulum is almost simultaneous, although the former is sometimes slightly

later than the latter. The lateral edge of the trochlea is generally narrow and often ill defined, in marked contrast to the smooth surfaces of the capitulum and lateral epicondyle. In fact, the latter is somewhat discoidal in shape and sometimes appears to belong to the capitulum rather than to the shaft of the bone.

In a girl aged 10 the three epiphyses were fused with each other, but the earliest instance in a boy, where they were fused on both sides, was at the age of 12. Union had taken place in half of the boys at the age of 13, but had not occurred on either side in a girl aged 16 nor on either side in a boy aged 15.

As Galstaun, unfortunately, had failed to note the union of the epiphyses of the capitulum to the lateral epicondyle and trochlea on each side prior to the union of the conjoint epiphysis to the shaft, his observations regarding these epiphyses will not be applicable for the purposes of comparison.

FUSION OF COMMON DISTAL EPIPHYSIS WITH DIAPHYSIS OF HUMERUS

		Instances in boys			Fusion in boys	
Age	Instances in girls	Author	Sidhom and Derry	Fusion in girls	Author	Sidhom and Derry
13	5	18	—	3	0	—
14	4	18	91	3	2	32
15	7	15	43	7	4	33
16	6	10	95	5	9	88

The earliest age at which union occurred was 13 years and 4 months in a girl and 14 years and 7 months in a boy. The majority showed fusion at the age of 13 in girls and 16 in boys, but instances of non-fusion were noted at the age of 16 in both sexes (on both sides in a female). Sidhom and Derry found the majority amongst Egyptian boys fused at the age of 15, that is a year earlier than in the Australian series.

EPIPHYSIS FOR THE MEDIAL EPICONDYLE

The medial epicondyle, unlike the lateral, is quite separate from the other centres at the lower end of the humerus and fuses directly and independently with the diaphysis.

The earliest age this has been noted is 3 years and 10 months in a female and 5 years and 9 months in the male. None of 23 boys aged 3 and 4 showed this epiphysis, although of 7 girls at these ages there were 3 examples. The centre was found in most girls at the age of 5 and in most boys at 6 years of age. Its absence was noted in a girl aged 6 and a boy aged 7.

The youngest girls where the medial epicondyle was found fused with the diaphysis were aged 10, the youngest boys 12, in one case being present on the right although fused on the left side. In one half of the girls union had taken place at the age of 14 and in one half of the boys at 16. An instance of

non-fusion was noted in a girl aged 16 (both sides) and in a boy aged 17 years and 0 months. Paterson gives the date of union as 18 to 21 in males, but in this series, in every one of 29 instances in males at these ages, it was already fused. Sidhom and Derry found amongst Egyptian boys that the majority had fused at the age of 16, that is about the same as in the Australian series,

	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
Age	Author	Galstaun	Author	Sidhom and Derry	Author	Galstaun	Author	Sidhom and Derry
3	4	—	9	—	2	—	0	—
4	3	—	14	—	1	—	0	—
5	17	—	12	—	16	—	5	—
6	8	—	8	—	7	—	5	—
7	8	—	15	—	8	—	14	—
10	7	—	18	—	4	—	18	—
11	3	—	12	—	3	—	12	—
12	1	—	21	—	1	—	19	—
13	5	7	15	—	3	0	14	—
14	3	24	15	101	2	6	14	95
15	7	16	16	39	0	1	16	29
16	6	12	10	98	3	2	5	41
17	5	16	16	95	0	0	7	15
18	5	9	10	68	0	0	0	6
19	4	3	8	24	0	0	0	1

but in one Egyptian boy union had not taken place at the age of 19 years and 3 months.

According to the results of Galstaun, it would appear that fusion does not take place earlier in Hindu than in Australian girls. Unfortunately, the Australian series is scarcely large enough for a true comparison.

EPIPHYSIS FOR THE TIP OF THE OLECRANON PROCESS

The main part of the olecranon process is formed by an extension upward from the diaphysis, a small wedge including the tip alone being formed from a separate centre, which may or may not comprise part of the articular surface of the greater semilunar notch. Generally there is only one centre, but often there are two or more.

	Instances in girls		Instances	Centres in girls		Centres
Age	Author	Galstaun	in boys	Author	Galstaun	in boys
6	9	—	15	1	—	0
7	9	—	16	0	—	1
8	12	—	19	7	—	3
9	4	—	11	4	—	3
10	7	—	18	3	—	15
11	5	—	12	5	—	8
12	2	—	27	2	—	26
13	4	7	15	3	7	14
14	4	24	18	1	14	17
15	8	16	18	0	2	16
16	5	12	5	3	0	2

The youngest subjects where epiphyses were present were a girl aged 6 and a boy aged 7. From the above it would appear that the epiphysis is present in a majority of girls at the age of 8 and of boys at the age of 10. Whilst fusion

takes place in the majority of girls at the age of 14, union does not occur in the majority of boys until 16 years of age. Instances of non-fusion were noted in a female at the age of 16 years and 0 months and in a male at 17 years and 6 months. The epiphyses had not yet appeared on either side in girls aged 10, but examples of absence, whether non-appearance or of fusion, can be noted at all ages in boys. The earliest to fuse was a girl aged 13. Absence of epiphyses may be noted at all ages in boys.

The much smaller Australian series suggests earlier fusion than is the case in Indian girls.

PROXIMAL EPIPHYSIS OF THE RADIUS

	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
Age	Author	Galstaun	Author	Sidhom and Derry	Author	Galstaun	Author	Sidhom and Derry
3	7	—	14	—	2	—	0	—
4	6	—	16	—	3	—	7	—
5	19	—	14	—	11	—	9	—
6	9	—	16	—	7	—	11	—
7	10	—	20	—	10	—	19	—
8	19	—	23	—	19	—	22	—
13	7	7	17	—	5	7	17	—
14	9	24	20	99	4	7	19	91
15	7	16	19	41	1	3	18	28
16	7	12	11	98	2	1	5	35
17	3	16	20	94	0	2	9	11
18	5	9	10	67	0	1	0	5

The earliest epiphysis noted was in a girl aged 3 years and 4 months and in a boy aged 4 years and 3 months. Davies and Parsons noted an instance in a girl aged 2. The majority of both sexes aged 5 showed the presence of this epiphysis. It was absent in girls aged 6 and in a boy aged 8.

The earliest age at which fusion had occurred was 13 in girls and 14 in a boy. Union had occurred in the majority of females at the age of 14 and of males at 16. One girl aged 16 showed non-fusion on both sides, whilst non-fusion on both sides was also noted in a boy aged 17 years and 6 months. Davies and Parsons found non-fusion in one subject at the age of 19 years.

Sidhom and Derry found the epiphysis of the majority of Egyptian boys fused at the age of 16 as above. In one instance it was not fused at the age of 18 years and 6 months.

Whilst in the Australian series were two instances in girls where fusion had occurred at the age of 13, in some Hindu girls this had not taken place at a later period than any of those of the Australians, in one instance at the age of 18.

In no case has a separate centre for the tubercle of the radius as described by Frazer been found.

DISTAL EPIPHYSIS OF RADIUS

The youngest female in whom this centre was seen was aged 10 months, where it was present on both sides, but it was not seen in any of 4 boys in their first year. One boy 1 year and 7 months old likewise showed no centre,

although present in 3 other boys in their second year. Cohn states that this epiphysis is constantly present at the age of 6 months, yet in 3 males, aged 10 months, 11 months and 1 year respectively, this was not the case. The centre was found in every one of eight instances in girls in their second year and in all of 19 instances of both sexes aged 2.

The youngest female in whom fusion had occurred was aged 16 years and 6 months, the youngest male 18 years and 5 months. The majority of females aged 18 and of males aged 19 showed union with the shafts. The oldest subjects

	Instances in females			Instances in males		
Age	Author	Pryor	Galstaun	Author	Pryor	Sidhom and Derry
Under 1	2	—	—	4	—	—
1	8	—	—	4	—	—
14	7	14	24	44	2	104
15	5	6	16	42	3	41
16	13	12	12	42	4	99
17	12	17	16	37	14	90
18	14	7	9	36	12	70
19	4	10	3	30	8	23
20	7	6	—	17	6	—
21	5	1	—	27	2	—
22	7	2	—	20	5	—
23	9	—	—	19	—	—

	Centres in females			Centres in males		
Age	Author	Pryor	Galstaun	Author	Pryor	Sidhom and Derry
Under 1	2	—	—	0	—	—
1	8	—	—	3	—	—
14	7	14	22	44	2	104
15	5	6	12	42	3	41
16	9	12	8	42	4	91
17	7	11	11	37	13	74
18	3	4	5	29	12	36
19	1	4	1	11	6	7
20	0	0	—	6	1	—
21	0	0	—	4	0	—
22	0	0	—	0	0	—
23	0	—	—	1	—	—

in whom union was not complete were a female aged 20 years and 5 months and a male aged 23.

Although there were six instances amongst 40 Hindu girls aged 14 and 15 in whom the centre had fused earlier than in any of the Australian series, only 15 out of 40 Hindu girls showed fusion between them of ages 16 and 19 compared with 23 out of 42 of the author's series. Although the majority of the Australian girls showed fusion at the age of 18, this was not the case amongst the Hindu girls until at least 19 years of age.

Sidhom and Derry found the majority of epiphyses in Egyptian boys united at the age of 19 as in the Australian series. In some instances union had occurred at the age of 16.

Like Galstaun, Pryor found union in American females at 19 and males at 20, that is later than in both the Australian and Egyptian series.

DISTAL EPIPHYSIS OF ULNA

The centre for this epiphysis was first seen at the age of 5 in each sex. Paterson reports it present in a girl aged 4. The epiphysis was present in the majority of girls at the age of 5 and boys at 6 years of age. The oldest girl in whom it was found absent was aged 7, and the oldest boy 8, except for an isolated instance in a boy aged 12.

The youngest female where this centre had fused was aged 16 years and 6 months, the youngest male 18 years and 5 months. It will be noted that

	Instances in females			Instances in males		
Age	Author	Pryor	Galstaun	Author	Pryor	Sidhom and Derry
5	3	—	—	7	—	—
6	7	—	—	11	—	—
7	6	—	—	23	—	—
8	11	—	—	12	—	—
13	10	2	—	35	3	—
14	7	14	24	44	2	104
15	5	6	16	42	3	41
16	12	12	12	41	4	94
17	11	17	16	33	14	87
18	14	7	9	34	12	69
19	4	10	3	29	8	24
20	8	6	—	16	6	—
21	5	1	—	27	2	—
22	8	2	—	20	5	—
23	19	—	—	17	—	—

	Centres in females			Centres in males		
Age	Author	Pryor	Galstaun	Author	Pryor	Sidhom and Derry
5	2	—	—	2	—	—
6	4	—	—	6	—	—
7	5	—	—	16	—	—
8	11	—	—	10	—	—
13	10	2	—	35	3	—
14	7	14	23	44	2	104
15	5	6	13	42	3	40
16	8	12	8	41	4	85
17	5	11	12	33	13	61
18	3	4	5	26	10	33
19	0	4	2	8	1	6
20	1	0	—	3	0	—
21	0	0	—	2	0	—
22	1	0	—	0	0	—
23	0	—	—	1	—	—

whilst the majority of epiphyses had fused at the age of 17 in females, it was not until the age of 19 that union was present in the majority of men. The oldest female in whom this centre had not yet fused was aged 22 and the oldest male 23. Paterson's conclusion, "it joins the shaft at the same time as the radius namely at 21 in males and a year earlier in females," implies a rather later date of fusion than is the case with the majority of the Australian series, although it is true that fusion of the lower epiphyses of the radius and ulna are almost simultaneous.

Similar remarks made in reference to the lower end of the radius would

also apply to the lower end of the ulna. Thus it would appear in Galstaun's Hindu series, that, with the exception of a few instances, fusion does not take place generally at an earlier age than in this Australian series of European descent.

Sidhom and Derry found that the majority of Egyptian males aged 18 show fusion, which is a year earlier than in the Australian series. In one boy fusion was present at the age of 15 years and 11 months.

Pryor found union in the majority of American girls at 16 and boys at 19, in each case earlier than in the Australian series, although the boys are later than in the Egyptian series.

STYLOID PROCESS OF THE ULNA

Borovansky and Hnevkovsky found a separate epiphysis for this process in a boy aged 5 years and 10 months on both sides. They report two instances of this epiphysis, one of which is illustrated.

In one boy aged 13 years and 10 months a separate ossicle representing the detached styloid process of the ulna was seen. This does not appear to have been caused by injury. In view of the frequency with which the styloid process is detached by trauma, it is important to recognise that this process may exist independently as a separate centre.

CARPAL BONES

These are all developed from a single centre as a rule. Woollard states that two centres have been found for the navicular, Pfitzner has described a double centre for the triquetrum, whilst Quain reports two centres being sometimes found for the lunate. In this series (see figs. 3 and 4) double centres for the lunate, one dorsal to the other, have been noted in a girl aged 6 and in boys aged 4 years and 7 months and 8 years respectively. Pryor has noted in a girl aged 7 years and 6 months a double centre for the multangulum minus on the right side, but not on the left. Borovansky and Hnevkovsky found these present on both sides in a boy aged 5 years and 10 months.

The order of appearance is by no means constant, for even in the same individual it may be different on each side. Thus, in a boy (see fig. 2) aged 6 years and 11 months, the multangulum majus was well marked on the left but completely absent on the right; the lunate had just appeared on the right side although no trace could be observed on the left. Pryor states that the order of appearance is a peculiarity of the family.

The first carpal bone to appear is usually the capitate, shortly followed by the hamate. Then follow the triquetrum, multangulum minus, lunate, multangulum majus, navicular and invariably last of all at a considerably later date, the pisiform, but there is considerable variation in the respective order of appearance of the lunate, multangula majus and minus and the navicular. In a female aged 3 months and a male aged 7 months, Pryor noted the appearance of the hamate before the capitate.

THE NAVICULAR

Age	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor
3	6	9	11	3	0	1	0	1
4	0	14	5	14	0	7	1	1
5	3	30	7	39	2	19	4	8
6	7	35	10	42	7	30	9	20
7	7	14	22	10	7	14	20	9
8	11	4	12	8	11	4	11	6

The earliest centres noted were in a boy aged 4 years and 6 months and girls aged 5. It was present in the majority of both sexes at the age of 5. The oldest subjects showing absence of centres were a girl aged 5 years and 5 months and a boy aged 8. Woollard states that two centres have been found for the navicular. This is important in considerations of fractures of this bone.

Pryor found this centre in a girl aged 3 years and 6 months and in a boy aged 4 years and 4 months. The majority of the girls aged 4 and boys aged 6 showed its presence. In his series it was not present in a girl aged 6 years and 4 months nor in a boy aged 8 years and 3 months.

THE LUNATE

Age	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor
1	6	3	5	2	0	0	1	0
2	9	4	10	2	3	1	1	0
3	6	9	8	3	2	5	4	0
4	0	14	5	14	0	13	3	10
5	3	30	8	39	3	26	6	31
6	7	35	9	42	7	30	8	20

This centre sometimes appears before the triquetrum and sometimes afterwards. The youngest subjects showing this centre were a boy in his second year and a girl aged 2 years and 7 months. It was found present in the majority of boys aged 4. Its absence was noted in a girl aged 3 years and 5 months, in one instance on both sides, and in a boy aged 6 years and 11 months, where it was present on the opposite side. On one side it was the only carpal bone absent except the pisiform.

Pryor found this centre in the majority of girls aged 3 and of boys aged 5. It was absent in a girl aged 6 years and 3 months.

In a girl aged 6 (see figs. 3 and 4) and boys aged 4 years and 7 months and 8 years respectively, two centres, one dorsal to the other, were noted for this bone. Pryor has noted on both sides in a boy aged 6 years and 4 months both the triquetrum and lunate to be possessed with double centres.

A small centre immediately alongside the lunate on the ulnar side is figured by Borovansky and Hnevkovsky, under the title "hypolunatum?"

THE TRIQUETRUM

	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
Age	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor
1	8	3	3	2	5	1	0	1
2	10	4	9	2	1	3	3	0
3	7	9	11	3	3	9	7	2
4	0	14	5	14	0	14	4	11
5	3	30	8	39	3	30	8	36

This centre is usually the earliest of the carpal bones to appear after the capitate and hamate, but may be preceded by the lunate. The earliest centres were noted in a female at the age of 1 year and 6 months and in males at the age of 2 (in one instance on both sides). It was found in the majority of boys aged 3. Its absence was noted in girls at the age of 3 and in a boy aged 4.

THE PISIFORM

This is the last of all the carpal bones to ossify, and is not always easy to detect when it first appears, as it frequently lies directly over the triquetrum, but a lateral or oblique view often shows its presence when it cannot be seen in the ordinary anterior view.

	Instances in girls		Instances in boys		Centres in girls		Centres in boys		
Age	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor	Paterson
7	6	14	25	11	0	1	2	0	
8	8	8	12	9	2	2	0	0	
9	5	4	6	8	2	2	1	0	
10	5	5	8	6	4	4	2	0	
11	6	3	14	5	6 100 %	3	8 61 %	1	25 %
12	14	2	17	5	13 100 %	2	11 73 %	2	55 %
13	12	0	34	3	12 100 %	0	26 86 %	2	80 %
14	8	0	45	1	8 100 %	0	38 92 %	0	100 %

The youngest boys noted with this centre were aged 7 and the youngest girl 8 years and 6 months. It was present in half of the girls at the age of 9 and the majority of boys at 11. The oldest girl in whom it was not present was aged 10 and the oldest boy 14 years and 7 months. Pryor found the centre present in a girl aged 7 years and 7 months, but absent in another girl aged 10 years and 7 months.

The percentages at each age are compared with the figures given by Paterson, the latter appearing to be a rough estimate only. In females, it was present in all of 40 instances at the ages 11 to 14, that is 100 per cent. Thus, in this series, this bone was rather more frequently demonstrable than is estimated by Paterson.

HAMATE

Except for the capitate, this is usually the first carpal bone to appear and was present in all babes of 10 months of both sexes and older, but was not present on either side in an infant aged 6 months. It was present in all four instances in babes aged 10 and 11 months. Davies and Parsons found it

absent in a child aged 1 year and 3 months. Pryor found it present in a child aged 3 months (female) and a male aged 7 months.

CAPITATE

This is the first carpal bone to appear. In one babe aged 6 months the centre for the capitate was present on both sides, although those for the hamate were absent. In a male child 1 week old the centre was not present. Pryor found it present in a male child aged 2 days, and in a female aged 4 days, but absent in a female aged 3 months and a male aged 7 months, in each case in the presence of the hamate.

MULTANGULUM MINUS

	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
Age	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor
3	6	9	9	3	1	1	0	0
4	0	14	5	14	0	7	1	0
5	4	30	5	39	4	24	2	9
6	7	33	9	41	7	28	7	18
7	6	14	26	10	6	14	25	7
8	10	4	10	8	10	4	9	7

The youngest girl showing this centre was aged 3 years and 5 months, where it was present on the right side but absent on the left, and the youngest boy was aged 4 years and 6 months. The centre was present in the majority of cases at the age of 5 in girls and 6 in boys. In a girl aged 3 years and 5 months it was absent, likewise in a boy aged 8. Pryor found it present in the majority of girls at the age of 4 and boys at 6. He found it absent in a girl aged 6 years and 7 months and in a boy aged 8 years and 3 months. He also found it duplicated in a girl aged 7 years and 6 months, whilst Borovansky and Hnevkovsky likewise found it duplicated in a boy aged 5 years and 10 months.

MULTANGULUM MAJUS

	Instances in girls		Instances in boys		Centres in girls		Centres in boys	
Age	Author	Pryor	Author	Pryor	Author	Pryor	Author	Pryor
3	6	9	9	3	1	0	0	0
4	0	14	4	14	0	6	0	5
5	3	30	6	39	3	20	5	11
6	6	33	9	41	6	26	7	15
7	6	14	24	10	6	14	23	8
8	10	4	9	8	10	4	8	6

The youngest girl showing this centre was aged 3 years and 5 months, the youngest boy 5. In one girl aged 3 it was not present on either side, whilst in a boy aged 8 it was found absent. In both sexes it was found in the majority of cases at the age of 5 years.

Pryor found the centre present in a boy aged 4 years and 1 month. He found it present in the majority of boys at the age of 7 and noted its absence in a girl aged 6 years and 7 months, and a boy aged 8 years and 10 months.

FIRST METACARPAL BONE

The epiphysis for this bone, unlike those of the other metacarpals, appears at the base instead of at the distal extremity. Additional centres also frequently are found for the distal extremity, in fact Borovansky and Hnevkovsky estimate that 50 per cent. of the boys of Prague present this epiphysis, whilst indications of its tendency may be noted in 70 per cent. by a fissure.

	Instances in females		Instances in males		Centres in females		Centres in males	
Age	Author	Galstaun	Author	Sidhom and Derry	Author	Galstaun	Author	Sidhom and Derry
1	6	—	4	—	5	—	0	—
2	10	—	7	—	7	—	4	—
3	6	—	7	—	6	—	5	—
13	12	—	28	—	11	—	28	—
14	3	24	42	110	2	13	40	100
15	5	16	41	42	3	6	37	28
16	13	12	37	101	0	1	28	32
17	10	16	43	96	0	3	25	10
18	19	9	33	71	0	1	4	5
19	5	2	37	24	0	0	2	0

The centre was seen earliest in a girl aged 1 year and 2 months and a boy aged 2 years and 6 months. It was present in the majority of girls during their second year and boys aged 2. Its absence was noted in a girl aged 2 years and 5 months and in boys aged 3.

The youngest female where the epiphysis had fused was aged 13, the youngest males 14. Fusion was complete in the majority of females at the age of 16 and the majority of males at 18. Fusion had not yet occurred in girls aged 15 nor in one man aged 19 years and 7 months.

SECOND, THIRD, FOURTH AND FIFTH METACARPAL BONES

The epiphyses for these usually appear, unlike those of the phalanges and the first metacarpal, at the distal extremities of the bones. Sometimes additional epiphyses appear at the proximal extremities of the second and very rarely of the fifth. Even when such a centre is not quite detached, an indication of such tendency is shown by the appearance of a constriction or fissure, instead of the usual epiphyseal interval. Epiphyses at the base of the second metacarpal were noted in a girl aged 3 and in a boy aged 7 years and 11 months. Very large epiphyses were present on each side in a boy aged 9 years and 8 months, who is the subject of cleidocranial dysostosis.

	Instances in girls					Instances in boys			
Age	Author				Galstaun				
1	1	1	3	3	—	3	1	3	3
2	8	8	9	9	—	6	6	6	6
3	4	4	5	5	—	5	6	6	6
14	2	2	2	2	24	24	23	26	28
15	8	8	8	8	16	19	21	20	21
16	11	9	9	8	12	22	23	21	20
17	7	6	9	11	16	26	27	28	30
18	17	16	14	18	9	27	26	28	25
19	3	3	4	4	3	30	30	26	29
20	8	8	10	11	—	16	18	18	18

Age	Centres in girls: Author				Centres in girls: Galstaun				Centres in boys			
1	1	1	1	1	—	—	—	—	2	1	1	1
2	7	7	6	6	—	—	—	—	5	4	4	2
3	4	4	5	5	—	—	—	—	5	5	5	5
14	2	2	2	2	10	10	9	9	24	23	26	28
15	5	7	6	6	7	7	7	7	19	21	20	21
16	2	1	1	1	1	1	1	1	21	22	20	18
17	1	1	1	1	4	4	4	4	16	18	21	22
18	1	0	0	0	1	1	1	1	6	6	7	6
19	0	0	0	0	0	0	0	0	3	3	2	2
20	0	0	0	0	—	—	—	—	1	1	0	0

The youngest subject with epiphyses for the fourth metacarpal was a girl aged 1 year and 10 months and for the fifth metacarpal 1 year and 5 months. In a female aged 1 year and 11 months centres for the first, second and third metacarpals were present, but those for the fourth and fifth were absent. In a boy in his second year centres were present for all metacarpals except the first. The epiphyses were present in the majority of both sexes during the second year for the second and third metacarpal bones and in the majority of both sexes for the fourth metacarpal at the age of 2. The majority of centres for the fifth metacarpal appear at the age of 2 in girls and 3 in boys. In a girl aged 2 years and 5 months and a boy aged 2 no centres were present in any of the metacarpals, whilst in another boy of 3 there were none for the middle, ring or little finger.

Except for the second metacarpal in a girl aged 14 years and 9 months the earliest to fuse in each of these metacarpals were in females at the age of 15 and in a male at 16 years. Union takes place in the majority of girls at 16 and boys at 18 years of age. In a girl aged 17 none of the centres for these bones had fused, and in another girl aged 18 the centre for the second metacarpal was still ununited. In 2 men aged 19 none of the centres for these metacarpal bones was united, whilst in another male of the same age the centre for the third metacarpal was still present although those for the second, fourth and fifth had fused with their respective diaphyses. Non-fusion of the second and third metacarpals was likewise present in a male aged 20 years and 7 months.

Palmer has found all the epiphyses for the metacarpal bones fused in the skeleton of a girl aged 14 years and 5 months.

Like Pryor, the author has not met with any example of a separate epiphysis for the styloid process of the third metacarpal bone mentioned by Cunningham and Morris.

According to Galstaun's figures, fusion appears to be complete in the majority of instances at the age of 14, which is 2 years earlier than is the case with the Australian series.

PHALANGES OF THE HAND

Paterson's statement that the phalangeal epiphyses appear "for all practical purposes in all three rows simultaneously," is not borne out by careful study, as the following account shows. Those for the thumb, for

instance, generally appear before the other phalanges. Nor are the other phalanges, even in the same row, always simultaneous in their genesis.

Paterson likewise reports that there are no cases of epiphyses in males before the third year, but in the proximal phalanges, at least, instances were seen in both sexes during the second year, and in a female infant of 10 months they were present in the proximal phalanx of the thumb as well as in the middle phalanges of the middle and ring fingers, although absent in the little finger. Davies and Parsons found the centre in each phalanx of the proximal row in an infant aged 9 months.

PROXIMAL PHALANX OF THE THUMB

Age	Instances in females	Instances in males	Centres in females	Centres in males
1	1	3	1	0
2	8	6	4	0
3	4	2	4	2
13	7	14	5	14
14	2	27	2	26
15	6	24	3	24
16	8	22	0	12
17	14	26	0	12
18	16	23	0	3
19	2	30	0	4

The earliest epiphyseal centres to appear were in a girl aged 1 year and 11 months and in a boy aged 3 years and 10 months. It was found in all six instances at 3 years of age. It was absent in a girl aged 2 years and 5 months where it was present in all the other proximal phalanges, and likewise was not present in a boy aged 2 years and 6 months. It was present in half the instances in girls at the age of 2.

The earliest centres to fuse were in a girl aged 13 years and 8 months and a boy aged 14. Fusion was complete in half of the instances in girls at the age of 15 and of boys at 17 years of age. The latest unfused were in a girl aged 15 years and 6 months and in a man aged 19 years and 11 months, in whom all the other phalanges of the row were found fused.

PROXIMAL PHALANGES OF INDEX, MIDDLE, RING AND LITTLE FINGERS

Age	Instances in girls				Instances in boys				Centres in girls				Centres in boys			
Under 1	0	1	2	2	1	1	1	1	0	1	1	1	0	0	0	0
1	3	2	2	3	2	2	2	2	3	2	2	2	2	2	2	2
2	7	6	7	5	5	5	5	6	7	6	7	5	4	4	4	4
3	4	4	4	4	2	3	3	3	4	4	4	4	2	3	2	2
13	6	8	7	7	8	6	6	7	5	7	7	6	8	6	6	7
14	4	2	2	3	18	17	19	19	4	1	1	2	17	16	18	18
15	8	8	7	5	19	18	18	18	7	5	4	3	17	17	17	18
16	6	11	11	8	21	22	19	20	1	1	2	1	18	18	16	17
17	6	4	2	9	27	27	28	23	0	0	0	0	15	16	14	15
18	16	13	14	14	25	29	26	24	0	0	0	0	4	4	3	4
19	3	3	3	2	28	28	30	30	0	0	0	0	3	2	2	2

These centres all appear considerably earlier than in the case of the thumb. The youngest female to show centres for these was aged 10 months, where they were present in the middle finger of the left hand and ring fingers

of both hands, but absent in the little fingers on both sides. The earliest centres for the index finger had appeared in a girl aged 1 year and 4 months and in a boy in his second year, whilst the earliest for the little finger were noted at 1 year and 10 months in a girl and in the second year in a boy. Davies and Parsons found the centres present in all the digits of the proximal row in a child aged 9 months.

In the majority of children of both sexes, centres had appeared in all four phalanges during their second year. In every instance centres were found in girls over the age of 10 months. In a boy aged 3 years centres for the ring and little fingers had not yet appeared.

The youngest subject with a fused epiphysis was a girl aged 13 years and 8 months in the case of the index and middle fingers and a girl aged 13 in the case of the little finger. In a girl of 14 it was fused in the middle, ring and little fingers, but not in the index. In a boy of 14 it was fused in all four digits. In the great majority of girls fusion was completed at the age of 16, and of boys at the age of 17 for the ring finger and 18 for the other digits. In a girl aged 16 fusion had not yet occurred in any of the four proximal phalanges. In a man aged 19 likewise none was fused, whilst in one man aged 19 years and 7 months the centre for the phalanx for the index finger was still present.

MIDDLE ROW OF PHALANGES

Age	Instances in females				Instances in males				Centres in females				Centres in males			
1	3	2	2	2	2	2	2	2	1	1	1	0	0	0	0	0
2	3	3	3	2	3	3	4	3	2	2	2	1	0	0	0	0
3	1	1	1	2	0	2	1	0	1	1	1	1	0	2	1	0
13	4	4	5	4	7	6	5	5	3	4	5	4	7	6	5	5
14	2	3	3	2	17	15	15	15	2	3	3	2	15	14	14	14
15	7	7	6	5	12	12	11	12	5	6	5	4	10	11	10	11
16	2	8	7	4	18	19	13	10	0	1	1	0	12	13	9	8
17	2	3	2	3	16	16	19	17	0	0	0	0	6	7	9	9
18	12	12	11	10	18	20	18	19	0	0	0	0	1	1	3	2
19	1	1	0	2	23	27	24	24	0	0	0	0	3	2	2	2

In the case of the index finger, the youngest girl with fused epiphysis was aged 13 years and 8 months. In a boy aged 14 the centres for the index, ring and little fingers had fused, although that for the middle finger had not yet united. The youngest boy with fused centre for the middle finger was aged 15. In a girl aged 15, all four epiphyses were fused, whilst the oldest girls with unfused centres for the middle and ring fingers were aged 16. The oldest males with unfused centres were aged 19 where they were present in the whole row. The majority of centres unite at the age of 16 in females and 17 in males except for the little finger which unites at 18.

DISTAL PHALANX OF THE THUMB

The youngest subject with a centre for this epiphysis was a female infant aged 10 months, where the centres were also present for the bases of the proximal phalanges of the middle and ring fingers. It was also seen in a male

infant, 1 year old, where none of the epiphyses for the middle row was present, although present in all of the proximal row except that for the thumb and all of the metacarpals except the first. The centre had not yet appeared in a female child 1 year and 10 months old nor in a male aged 2.

		Instances in males			Centres in males	
Age	Instances in females	Author	Sidhom and Derry	Centres in females	Author	Sidhom and Derry
13	4	5	—	2	5	—
14	2	15	102	1	14	86
15	6	14	40	2	13	15
16	6	10	95	0	7	15
17	4	26	90	0	8	9
18	12	15	70	0	1	3
19	3	29	—	0	3	—

The earliest centres to fuse were at the age of 13 years and 8 months in a girl and 14 in a boy. Half had fused at the age of 13 in females and the majority at 17 in males. The oldest female with unfused epiphysis was aged 15 and the oldest male 19 years and 7 months.

Sidhom and Derry found fusion to take place in the majority of Egyptian boys at the age of 15, that is two years earlier than the Australian series.

DISTAL PHALANGES OF INDEX, MIDDLE AND RING FINGERS

In a girl aged 1 year and 11 months the centres were present in the middle and ring fingers but absent in the index and little fingers. In a boy aged 2 the epiphyseal centre was present in the index finger on one side only, but absent on the other side as well as in all the other distal phalanges on both sides. One child aged 3 showed no epiphyses in any of these fingers. In a boy aged 2 years and 6 months the centre for the ring finger had not yet appeared.

	Instances in females				Instances in males				Centres in females				Centres in males			
Age																
14	2	3	3	3	14	11	12	12	1	2	2	3	13	10	11	11
15	7	7	7	5	6	7	8	9	3	2	2	2	5	6	8	8
16	6	6	7	4	8	12	8	9	0	0	1	0	5	5	7	7
17	4	2	3	4	14	14	16	16	0	0	0	0	6	6	6	7

In a girl aged 14 years and 9 months the centre for the index finger had fused. In a boy aged 14 the centres for all these phalanges had fused, whilst in a girl of the same age the centres for the epiphyses of the middle and ring fingers had united with the diaphyses. In a girl aged 15 years and 6 months the centres were fused in the case of all the digits. In the female the majority of the epiphyses fuse at the age of 15, in the male at 16 for the middle finger and 17 for the index, ring and little fingers. Thus it appears that the centre for the middle finger fuses at an earlier date than the others in the male at least. Unfused epiphyses were present for all fingers at the age of 15 in females, and for the ring finger in a girl aged 16, whilst the oldest male with non-fusion for all the distal phalanges (both sides) was aged 17.

SESAMOID OSSICLES

Sesamoid ossicles, usually two, are practically constantly found over the heads of the first metacarpal bones on the palmar aspect. Similar ossicles, usually single, are generally, but not invariably, found over the heads of the second metacarpal on the radial side and the fifth metacarpal bone on the ulnar aspect, but similar ossicles over the third and fourth are rather rare. Usually, also, very much smaller ossicles are present in the tendon of the flexor longus pollicis beneath the head of the proximal phalanx of the thumb, and these are always single.

PROXIMAL SESAMOID BONES OF THUMB

Age	Instances in females	Instances in males	Centres in females	Centres in males
11	2	5	2	0
12	5	4	2	0
13	3	1	3	0
14	2	10	2	9
15	5	16	5	15

The earliest instances were noted in a girl aged 11 years and 5 months and a boy aged 14 years and 5 months, the majority of girls aged 13 and of boys aged 14 showing sesamoids. It was absent on both sides in girls aged 12 and also absent in a boy aged 15. It was likewise noted absent in a subject aged 17 of unknown sex.

SESAMOID OF INDEX FINGER

Age	Instances in females	Instances in males	Sesamoids in females	Sesamoids in males
11	3	1	1	0
12	4	2	1	0
13	3	1	0	0
14	1	7	0	2
15	6	5	3	2
16	4	8	4	5
17	3	11	3	3
18	5	14	1	5
19	3	16	1	9
20	5	9	4	5
21	2	11	2	9
22	2	11	1	5
23	6	9	3	8
24	1	7	1	4
25	0	3	0	2
26	0	1	0	0
27	0	1	0	0
28	0	1	0	1

The earliest examples were noted in a girl aged 11 years and 6 months. It is present in half of the girls at 15 and the majority of young men at 19. However, it is commonly absent at a much later date; thus it was not present on either side in a woman of 23 although present over the fifth metacarpals, nor was it present in a man aged 27. Older subjects were not studied, but it is likely that in certain individuals it may never appear.

SESAMOIDS OF MIDDLE AND RING FINGERS

These are rare. An instance was noted in a girl aged 13 years and 10 months. In a man aged 21 (fig. 5) sesamoid bones were present at the heads of all the metacarpals, those for the middle and ring fingers being on the radial aspects, whilst two were present for the fifth metacarpal. In another subject (fig. 6) of the same age of unknown sex a very large sesamoid appeared to be situated over the middle of the head of the third metacarpal bone.

SESAMOID OF LITTLE FINGER

Age	Instances in females	Instances in males	Sesamoids in females	Sesamoids in males
13	5	1	1	0
14	0	6	0	0
15	5	11	4	4
16	4	10	4	4
17	4	13	4	6
18	4	21	3	12
19	3	15	2	10
20	8	9	8	5
21	3	11	3	10
22	6	13	5	9
23	6	13	5	13
24	3	6	3	4
25	0	4	0	4
26	0	4	0	2
28	0	1	0	1

The earliest examples were seen at the age of 13 years and 10 months in the female and 15 years and 0 months in a male. At the age of 15 in the female and 18 in the male the majority showed presence of these ossicles. However, instances were found at the age of 23 in the female and 27 in the male where they were not present.

DISTAL SESAMOID OF THUMB

This is a very small ossicle found at the head of the proximal phalanx of the thumb.

Age	Instances in females	Instances in males	Sesamoids in females	Sesamoids in males
15	0	6	0	2
16	3	4	3	2
17	2	7	2	5
18	3	8	3	5
19	1	8	0	6
20	3	4	2	4
21	0	6	0	5
22	1	3	1	2
23	0	7	0	5
24	0	4	0	1
25	0	1	0	1
26	0	1	0	1

The earliest sesamoids were seen at the age of 15 in boys and 16 years and 3 months in a girl. The majority of females aged 16 and half of the males aged 16 showed its presence. Examples of absence were noted at the age of 20 in the female and 24 in the male.

UNION OF ILIUM, ISCHIUM AND PUBIS

Age	Instances in females	Instances in males	Fusions in females	Fusions in males
10	2	8	2	0
11	10	10	2	0
12	7	13	1	0
13	4	5	2	3
14	7	10	4	7
15	9	12	9	8
16	12	8	11	6

The youngest girl in whom the cartilaginous junction (Y-shaped cartilage) of the three component parts of the os coxae had completely ossified was aged 10 years and 6 months and the youngest boy 13, in each case on both sides. Fusion had taken place in half of the girls at the age of 13 and the majority of boys not until 15 years of age. The oldest subjects with unfused centres were a boy aged 16 years and 3 months and a girl aged 16 years and 10 months.

UNION OF ASCENDING ISCHIAL WITH DESCENDING PUBIC RAMUS

In the ordinary antero-posterior view of the pelvis these rami are seen obliquely where they form the lateral boundaries of the perineum. The descending pubic ramus before fusion with the ischium forms a rounded protuberance somewhat overlapping the ischium, thus making it difficult to be sure in many cases whether union has actually taken place or not.

Age	Instances in females	Instances in males	Fusions in females	Fusions in males
3	15	20	2	0
4	10	12	2	0
5	6	23	4	7
6	1	9	0	2
7	8	20	4	11
8	9	8	8	3
9	7	5	7	4
10	1	8	1	6
11	6	8	5	8

The youngest girl showing fusion of the rami was aged 3 years and 11 months, the youngest boy 5 years and 9 months, on both sides in each case. Half showed union at the age of 7 in girls and the majority at the age of 9 in boys. Davies and Parsons noted fusion in a boy aged 3. In a boy aged 10 union was not complete on either side, but in a girl of 11 fusion was present on one side but not on the other.

EPIPHYSIS FOR THE ILIAC CREST

This varies greatly in length, and frequently consists of several detached fragments.

Age	Instances in females	Instances in males	Centres in females	Centres in males
14	6	7	5	0
15	11	5	11	2
16	16	8	16	5
17	14	15	10	10
18	26	20	24	14
19	13	18	7	13
20	28	12	15	6
21	17	17	6	3

The youngest subjects in whom these epiphyses were present were a girl aged 14 and a boy aged 15, where it was present on each side in each case. In females the majority of epiphyses appear at the age of 14 and in males at 16 years of age, but the maximum incidence is at 15 and 16 in girls and 18 in young men. Epiphyses were found present in females on both sides at the age of 21, and in the male at the age of 21 years and 7 months.

SYMPHYSIS PUBIS

An epiphysis for the symphysis such as is usually described by anatomists has not been found. The nearest approach was in a male subject aged 18 (see fig. 7), but this appears to be a forward extension of an epiphysis which may be found at any part of the perineal margin reaching from the tuber ischii to the lower margin of the symphysis. The epiphysis therefore, as is usually described, either does not exist or is very rare. Similarly no trace of any epiphysis about the pubic crest or pubic spine has been met with.

EPIPHYSIS FOR THE ANTERIOR SUPERIOR ILIAC SPINE

This appears to be a rare epiphysis and in this series was only met with twice, each time in females aged 14 and 17 respectively, in one of whom, at least, it was present on both sides. Possibly this epiphysis might be considered a separate fragment of the epiphysis for the iliac crest (see figs. 8 and 9).

EPIPHYSIS FOR THE TUBER ISCHII

The epiphysis for this process forms a thin scale of bone of variable size. Sometimes it extends forwards forming a thin scale along the ascending ramus of the ischium and descending ramus of the pubis even as far as the apex of the perineal triangle (see note concerning epiphysis for the symphysis). This is the epiphysis described by Stevenson as the ramal epiphysis which he regards as distinct from that of the tuber ischii (see fig. 7).

Age	Instances in females	Instances in males	Centres in females	Centres in males
13	4	7	2	1
14	6	12	2	0
15	2	12	0	1
16	7	8	6	0
17	3	12	2	4
18	10	14	6	5
19	7	13	6	8
20	21	10	18	2
21	4	11	2	3
22	20	8	3	0
23	6	9	0	0
24	15	11	2	0

The youngest boy in whom this centre was found was aged 13, and the youngest girl 13 years and 5 months, in each case being present on both sides. The above table appears to indicate that the epiphysis is present in the majority of females at the age of 16 and of males at the age of 19. The maximum incidence is at the age of 19 in both sexes. Fusion is present in the majority of males at the age of 20 and in half the females at 21. It seems to be much less frequently demonstrable between the ages of 13 to 24 in males (24 times in 127 instances = 18·9 per cent.) than in females (49 times in 105 instances = 46·6 per cent.). It was present on both sides in a man aged 21 and a woman aged 24.

HEAD OF FEMUR

The epiphysis for the head of the femur apparently always appears during the first year after birth. It was present in a male infant aged 6 months, but in each of two boys aged 9 months it was present on the right side, although absent on the left. A girl aged 10 months showed the centre on both sides. In all of five instances in boys and 19 in girls in their second year the centre was found. Davies and Parsons noted its presence in a girl aged 6 months, whilst Borovansky and Hnevkovsky found the centre in a boy aged 3 weeks.

Age	Instances in females	Instances in males	Centres in females	Centres in males
14	7	10	0	9
15	5	8	0	5
16	11	10	1	6
17	5	12	0	4
18	10	14	0	0
19	6	19	0	0
20	21	10	0	2

The youngest to fuse in each sex were girls aged 14 and a boy of 14, in the former instances on both sides. At the age of 14 the great majority had fused in girls, but not until the age of 17 in males had the majority united. This is much earlier than the dates given by Paterson, namely 17 for females and 18 for males. The oldest subjects with unfused epiphyses were 16 years and 10 months in a female and 20 years and 2 months in a male (both sides).

EPIPHYSIS FOR GREATER TROCHANTER

Age	Instances in females	Instances in males	Centres in females	Centres in males
2	10	12	2	0
3	15	18	9	0
4	10	10	4	3
5	8	21	8	16
6	6	4	6	2
14	7	9	0	9
15	2	5	0	2
16	6	4	1	3
17	3	9	0	4

The youngest girl with a centre for the greater trochanter was aged 2, where it was present on both sides, whilst the youngest boy was aged 4 years and 4 months. The majority of epiphyses appeared in both sexes at the age of 5 years. Borovansky and Hnevkovsky found this centre present in a boy aged 3 years and 5 months. The oldest girls in whom the epiphyses had not yet appeared on either side were aged 4, whilst in a boy of 6 the epiphyses were likewise absent on both sides.

The earliest to fuse were girls aged 14 and a boy of 15, in each case on both sides. The majority were fused in girls at the age of 14 and half in boys at 17. Union had not yet taken place in a girl aged 16 years and 10 months nor in a boy aged 17 on either side.

EPIPHYSIS FOR LESSER TROCHANTER

Age	Instances in females	Instances in males	Centres in females	Centres in males
10	0	9	0	1
11	9	10	3	0
12	5	9	0	6
13	4	4	0	0
14	5	13	0	11
15	4	7	0	4
16	7	8	1	4
17	3	10	0	2

The youngest girls with epiphyses for this process were aged 11 (in one on both sides) and the youngest boy 10 years and 9 months, where it was present on the left side but not on the right. At the age of 14 it was present in boys in the great majority of cases. The maximum incidence was in girls at the age of 11 and boys at the age of 14. Although the centre was present in 28 of 70 instances in boys aged 10 to 17, it was only noted four times in 39 instances in girls of the same ages. It seems probable that this centre is not constantly present and perhaps is much more common in boys than in girls. The centre was found present in a girl aged 16 years and 10 months, and in boys aged 17. It was likewise found in a female aged 24, but no explanation can be given for this extreme delay in union.

DISTAL EPIPHYSIS OF FEMUR

The centre for the distal extremity of the femur was found in every infant examined, including 13 in their first year. It usually appears before birth.

Pryor noted the presence of epiphyses in each of 2 females within 2 days after premature birth at 8 months, but it was not present in a male under similar circumstances. Of 43 boys and 48 girls during the first 9 days after birth, this epiphysis was present in every instance except 2 boys.

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
14	5	8	4	8
15	6	8	3	8
16	7	12	4	10
17	6	17	0	11
18	8	11	1	6
19	4	12	1	1

The youngest girl in whom this epiphysis had fused was aged 14, the youngest boys 16. The centre was fused in the majority of females at the age of 17 and in the majority of males at 19. Instances of non-fusion were met with in both sexes at the age of 19.

THE PATELLA

This bone is best demonstrated in young children in the lateral view of the knee joint, for its absence cannot always be determined in the postero-anterior view as the bone may be hidden over the shadow of the lower end of the femur.

Sometimes an additional centre on the upper and outer aspect is present. This forms the patella bipartita or patellula. Borovansky and Hnevkovsky found one in a boy aged 14. In this series an example was seen in a female aged 27 years and 6 months. Borovansky and Hnevkovsky also figure a separate ossicle at the apex of the patella in a boy aged 16 years and 11 months.

Age	Instances in females	Instances in males	Centres in females	Centres in males
2	5	6	1	0
3	2	4	1	0
4	1	6	1	2
5	6	3	6	3
6	1	4	1	4
7	2	7	2	7
8	1	7	1	6

The youngest girl showing a centre for the patella was aged 2 years and 6 months, the youngest boy 3 years and 11 months. It was present in the majority of girls from the age of 3 and of boys at the age of 5. In a girl aged 3 years and 0 months and a boy aged 8 the bone had not yet appeared. Borovansky and Hnevkovsky found a centre present in a boy aged 3 years and 7 months.

THE FABELLA

Of this series the youngest female showing this sesamoid bone was aged 17, the youngest male being 16 years and 5 months of age. It is by no means common, for of 160 knees of individuals aged 16 to 29 it was present in 16 instances only, that is in 10 per cent.

The author has learnt of an instance where this ossicle was removed surgically under the impression that it was a pathological foreign body.

PROXIMAL EPIPHYSIS OF THE TIBIA

This was present in every infant examined and usually appears before birth.

Pryor noted this centre present 2 days after premature birth at 8 months in a female, but was absent in a male and a female after premature birth at 8 months. Of 47 female and 42 male infants in the first 9 days after birth this centre was noted absent in 7 females and 13 males, being relatively twice as frequently absent in boys as in girls. Its absence was also noted in a girl aged 25 days.

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
14	6	8	5	8
15	5	9	2	9
16	7	10	1	8
17	6	17	0	11
18	10	10	1	4
19	4	16	1	2

The tongue-shaped prolongation which forms the anterior tubercle is not usually present until after the age of 8. Usually it is an extension of the proximal epiphysis forward over the upper end of the diaphysis. Sometimes an additional centre is present over this process.

The earliest to fuse were in a girl aged 14 and a boy aged 16 (both sides). Although the centre had disappeared in the majority of girls at the age of 15, it was not until the age of 18 that the majority of epiphyses in boys had united. Instances of non-fusion were found in both sexes at the age of 19.

PROXIMAL EPIPHYSIS OF THE FIBULA

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
3	5	9	3	3
4	6	12	5	5
5	7	5	7	4
14	5	7	4	7
15	4	10	1	10
16	6	10	4	8
17	6	16	0	11
18	9	11	1	7
19	5	14	0	1

The earliest centres noted were in a girl aged 3 years and 11 months and on both sides in a boy aged 3 years and 4 months. Paterson records its presence in a girl aged 2. It was present in the majority of girls at the age of 3 and of boys at 5. Its absence was noted in a girl aged 4 and a boy aged 5.

The earliest epiphyses to fuse were in a girl aged 14 and a boy aged 16. The majority were fused at the age of 17 in females and 19 in males. The oldest subjects in whom fusion had not yet occurred were a female aged 18 and a male aged 19.

DISTAL EPIPHYSIS OF THE TIBIA

This was found to be present in every infant examined including a girl aged 7 months (both sides) and a boy aged 9 months. Borovansky and Hnevkovsky found its presence in a boy aged 3 months and 3 weeks.

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
13	13	7	12	7
14	5	19	2	19
15	6	12	0	10
16	10	8	3	6
17	5	22	0	7
18	8	14	0	1

The youngest girl to show fusion of this epiphysis was aged 13 and the youngest boys 15. The above table shows that the majority of epiphyses fuse at the age of 14 in girls and 17 in boys. Instances of non-fusion were noted in a female aged 16 years and 4 months and a male aged 18.

As is the case with the distal epiphysis of the radius and ulna, so are the distal tibial and fibular centres fused approximately simultaneously with the shaft. However, in the girl of 13 quoted above, although the centre for the distal end of the tibia had fused, that for the fibula had not yet done so, being thus a violation of the oft-quoted rule that the first epiphyses to appear are the last to unite.

In a male aged 17 years and 7 months an ossicle was seen on both sides at the tips of the medial malleoli, and is clearly demonstrable in both the antero-posterior and lateral views. The author can nowhere find a record of such an ossicle in the literature. The term os malleoli medialis is suggested.

DISTAL EPIPHYSIS OF THE FIBULA

This was found present on both sides in a female infant aged 11 months, and was likewise found in a boy aged 9 months, but was not present in a girl of 7 months nor in a boy aged 1 year and 8 months, although present in 3 of 4 boys and all of 5 girls during their second year.

Age	Instances in females	Instances in males	Centres in females	Centres in males
14	5	18	2	18
15	6	12	0	10
16	10	10	3	8
17	5	21	0	6
18	7	13	0	1

The earliest epiphyses to fuse were found in a girl aged 14 years and 10 months and boys aged 15. The majority had united in girls at the age of 14 and in boys at 17. Instances of non-fusion were noted in a girl aged 16 years and 4 months and in a boy aged 18.

TARSAL BONES

No infant was found in which the centres for the talus, calcaneum, cuboid or third cuneiform had not already appeared. The calcaneum usually has an additional apophysis for the posterior aspect of the heel. The other tarsal bones usually ossify from a single centre, but sometimes the talus has a separate centre for the medial tubercle, which, when it fails to unite with the primary centre, forms the os trigonum. In this series, both the navicular and the first cuneiform have been noted arising from two centres.

Pryor found centres for both calcaneum and talus present in all of 3 premature 8 months' babes of both sexes, as well as in all of 90 other infants of both sexes during the first 9 months after birth.

APOPHYSIS OF THE CALCANEUM

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
7	3	6	1	1
8	2	6	2	3
12	1	6	0	6
13	12	8	9	8
14	4	16	1	15
15	7	6	0	4
16	10	14	2	7
17	3	18	0	2
18	7	10	0	1

The earliest centres to appear were in a girl aged 7 years and a boy aged 7 years and 5 months. Borovansky and Hnevkovsky noted the centre in a boy aged 6 years and 2 months. It was absent in a girl aged 7 and in a boy aged 8 years and 7 months, but was present in all of 16 instances in children aged 9 to 11 years.

The earliest to fuse with the primary centre were a girl aged 12 years and 10 months and boys aged 15. The apophyses were fused in the majority of girls aged 14 and in half of the boys aged 16. The oldest subjects with ununited apophyses were a female aged 14 and a male aged 18.

THE CUBOID

A centre for this bone was present in every foot in the series examined.

Pryor found it present in a female 2 days after premature birth at 8 months, but was absent in another female and in a male, both also prematurely born at 8 months. He also examined 89 infants, 42 males and 47 females, during the first 9 days after birth and found the centre present in 31 females and 11 males, that is approximately 64 per cent. in girls and 25 per cent. in boys. It was, however, found absent in a boy aged 13 days and in a girl aged 25 days.

TARSAL NAVICULAR

Age	Instances in girls	Instances in boys	Centres in girls	Centres in boys
1	3	2	3	0
2	7	7	5	3
3	8	8	7	7
4	6	7	6	7
5	3	10	3	9

The youngest girl with centre for the navicular was aged 1 year and 3 months, the youngest boy 2 years and 6 months. In a girl aged 3 and a boy aged 5 the centre had not yet appeared. The centre was present in the majority of girls during their second year and of boys at the age of 3.

In a boy aged 3 two centres were present for this bone.

FIRST CUNEIFORM

Age	Instances in females	Instances in males	Centres in females	Centres in males
1	2	1	2	0
2	8	5	8	3

The youngest female with centre for this bone was aged 1 year and 8 months, the youngest males 2 years and 6 months. Davies and Parsons found it present in a girl aged 12 months. It was found present in the majority of instances in girls during their second year and in boys aged 2. Its absence was noted in a girl aged 11 months and a boy aged 2 years and 2 months. Although Woollard has stated that a double centre for this bone has not been satisfactorily demonstrated in a roentgenograph, an instance of two centres is noted in a girl aged 2 years and 3 months (fig. 10).

SECOND CUNEIFORM

Age	Instances in females	Instances in males	Centres in females	Centres in males
1	2	1	2	0
2	7	5	6	2

As with the first cuneiform, the youngest girl with a centre was aged 1 year and 8 months, the youngest boy being aged 2 years. In a boy aged 2 years and 6 months it was absent although present in the first cuneiform. It was found absent in a girl aged 2 years and 6 months on the right side, although present on the left, as well as in another boy aged 2. Davies and Parsons noted the absence of this bone in a child aged 3. It was present in the majority of girls during the second year and in half of the boys at the age of 2.

THIRD CUNEIFORM

The centre for this bone was found in every infant examined, even when the first and second cuneiforms were absent. Davies and Parsons noted its presence at the age of 4 months. It certainly appears before the other cuneiforms and the navicular.

FIRST METATARSAL

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
2	6	4	5	2
3	5	4	5	3
14	1	7	0	7
15	3	4	0	3
16	7	10	2	8
17	3	16	0	3
18	5	9	1	1

The earliest epiphyses to appear were in a girl aged 2 years and 6 months (both sides) and in a boy also aged 2 years and 6 months. In the former it was present on both sides in the first, second and third, but not in the fourth and fifth metatarsals, in the latter absent in the four other metatarsals. In another girl aged 2 years and 7 months it was also present in the first but absent in all the others. The centre was absent in a girl aged 2 years and 4 months and in a boy aged 3 years and 6 months. It was present in the majority of instances in girls and half of those in boys at the age of 2. Davies and Parsons report the presence of an epiphysis in a female aged 10 months.

The earliest to fuse were in a girl aged 14 and a boy aged 15. Although the majority of girls aged 14 showed fusion, it was not until the age of 17 years that this was the case in boys. Instances of non-fusion were found at the age of 18 in both sexes.

SESAMOID BONES OF HALLUX

These are usually present beneath the head of the first metatarsal bone on the plantar aspect. The medial sesamoid is frequently split into two by a transverse fissure as though it were fractured. Occasionally the lateral sesamoid is similarly split. These ossicles were found at the age of 13 years and 4 months in a girl and 14 in boys. Borovansky and Hnevkovsky found these present in a boy aged between $11\frac{1}{2}$ and $12\frac{1}{2}$ years.

SESAMOID BONE OF FIFTH METATARSAL

The only instance of this was seen on both sides in a woman aged 21 years and 10 months.

EPIPHYSES FOR SECOND, THIRD, FOURTH AND FIFTH METATARSAL BONES

Age	Instances in girls				Instances in boys				Epiphyses in girls				Epiphyses in boys			
2	6	6	6	6	3	1	3	3	2	2	0	0	0	0	0	0
3	3	3	3	3	1	1	1	1	3	3	1	1	0	0	0	0
4	1	1	1	1	3	3	3	3	1	1	1	1	3	3	2	1
14	1	1	1	1	7	7	6	6	0	0	0	0	7	7	6	6
15	5	5	5	5	5	5	5	5	0	0	0	0	3	3	3	3
16	7	7	7	6	11	12	11	8	1	3	1	1	9	10	9	6
17	4	3	3	3	13	13	16	15	0	0	0	0	1	1	3	3
18	5	5	5	5	8	8	7	7	1	1	1	1	0	0	1	1

In a girl aged 2 years and 6 months centres were present on both sides for the heads of the second and third metatarsal bones, but had not yet appeared for the fourth and fifth. In a female aged 3 years and 11 months, centres for all five metatarsals were present. In a boy aged 4 those for the first, second, third and fourth metatarsals were present, but that for the fifth had not yet appeared. In another boy aged 4 years and 6 months on the right side, centres were present for all five metatarsals, but on the left, although present for the first, second and third, were absent for the fourth and fifth. In a girl aged 2 years and 7 months, and in a boy aged 2 years and 6 months, although

centres were present for the first, epiphyses were absent for all the other metatarsal bones.

The youngest subjects in whom the epiphyses were found fused in all four outer metatarsal bones were a girl aged 14 and a boy aged 15. In a male aged 17 years centres were present in all five metatarsal bones. They were likewise present in a female aged 18. In a male of the same age they were absent in the case of the second and third metatarsal bones although present for the fourth and fifth. Fusion was complete in the majority of girls at the age of 15 and of boys at 17 years of age.

EPIPHYSIS AT BASE OF FIFTH METATARSAL BONE

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
12	2	3	1	0
13	8	1	2	0
14	1	9	0	5

Sometimes an epiphysis is seen at the base of the fifth metatarsal bone. When this fails to unite with the shaft, it has been described as the os vesalii, which, according to Woollard, has only been recorded four times in roentgenographic pictures. The youngest female with such an epiphysis was aged 12, the youngest male 14, but instances were noted at the age of 17 in subjects of unknown sex. Its maximum incidence in males at least appears to be at the age of 14 when it was present in 5 of 9 instances. Altogether it occurred 11 times in 70 subjects between the ages of 12 and 17. It is evidently not constantly present. Borovansky and Hnevkovsky noted a centre in a boy aged 11 years and 7 months.

PROXIMAL PHALANX OF HALLUX

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
2	5	3	4	1
14	1	5	0	5
15	5	5	0	3
16	6	13	1	11
17	3	15	0	3
18	5	7	1	0

The epiphysis at the base of the phalanx was found in a girl and a boy, each at the age of 2 years and 6 months. In a girl aged 2 years and 4 months it was absent although present in the other phalanges of the row, whilst it was absent in all five proximal phalanges in a boy aged 2 years and 6 months.

The youngest subjects in whom this epiphysis was found fused were a girl aged 14 and a boy aged 15. Fusion had taken place in the majority of girls at the age of 14 and of boys at 17 years of age. Non-fusion was present in a male aged 17 (although fusion was complete in all the other proximal phalanges) and in a female aged 18.

PROXIMAL PHALANGES OF SECOND, THIRD, FOURTH AND FIFTH TOES

Age	Instances in girls				Instances in boys				Epiphyses in girls				Epiphyses in boys			
2	5	5	5	4	3	3	3	3	4	4	4	3	2	2	2	2
14	1	1	1	1	5	5	5	6	0	0	0	0	5	5	5	6
15	5	5	4	4	5	5	5	5	0	0	0	0	3	3	3	3
16	6	6	6	7	11	12	11	10	0	0	0	1	9	10	9	7
17	4	3	3	3	14	14	14	14	0	0	0	0	2	1	1	2
18	5	5	6	6	8	7	7	7	1	1	1	1	0	0	0	1

The epiphyses at the bases of the proximal phalanges were found in a girl aged 2 years and 4 months and in a boy aged 3 years and 2 months. In a boy aged 2 years and 6 months, and in a girl aged 2 years and 7 months, it had not yet appeared in any of the toes.

The youngest subjects in whom these were found fused with the shafts were a girl aged 14 and a boy 15 years of age. As with the metatarsals, the centres were fused in the majority of girls at the age of 14 and of boys at 17 years of age. In a boy of 17 non-fusion was present in all four digits. This was likewise the case in a girl aged 18. In a male aged 18, although fusion was present in the case of the second, third, and fourth toes, that for the little toe was still ununited.

MIDDLE ROW OF PHALANGES

As the various epiphyses of the middle row of phalanges develop at different periods, these will be described in separate groups.

MIDDLE PHALANGES OF SECOND TOE

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
2	3	1	1	0
3	3	1	2	1
4	1	2	1	2
5	0	3	0	2
6	1	0	1	0
7	1	2	1	0
8	0	4	0	2
12	1	1	0	1
13	5	2	3	2
14	0	5	0	5
15	4	4	0	1
16	6	9	0	6
17	2	10	0	0
18	2	7	1	0

Earliest centres were found in a girl aged 2 years and 4 months where it was present in the whole row, and in a boy aged 3, where it was also present in the third, but absent in the fourth and fifth toes. It was not present in a girl aged 3, although present in the other phalanges of the row, whilst in a boy aged 8 years and 7 months it was not present in any of the middle phalanges. It was present in the majority of girls at the age of 3 and of boys at the age of 4.

MIDDLE PHALANGES OF THIRD AND FOURTH TOES

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
2	2 3	1 1	1 1	0 0
3	3 3	1 1	3 3	1 0
4	1 1	2 2	1 1	0 0
5	0 0	3 4	0 0	2 3
6	1 1	1 0	0 0	1 0
7	1 1	2 2	0 0	0 0
8	0 0	4 4	0 0	2 2
9	0 0	0 0	0 0	0 0
10	0 0	2 3	0 0	1 1
11	0 1	1 1	0 0	1 0
12	2 1	1 0	0 0	1 0
13	5 4	2 2	1 0	0 0
14	0 0	5 3	0 0	2 0
15	4 2	4 4	0 0	1 0
16	6 6	9 7	0 0	3 1
17	2 2	11 10	0 0	0 0
18	3 4	5 6	1 0	0 0

These being vestigial phalanges, the development of their epiphyses is quite different to the others. They were both present in a girl aged 2 years and 4 months. In a boy aged 3 that for the third toe was present although absent for the fourth toe. In a boy aged 5 years and 2 months they were present in each case on both sides. Their presence was noted at various ages right up to adult life. They appeared to be present in the majority of females at the age of 3 and of males at the age of 5.

The oldest subjects in whom these were present was a male aged 16 and a female aged 18, where it was present in the third, but absent in the fourth toe. The absence of these epiphyses may be noted in one of the three following circumstances: (*a*) stage before appearance of epiphysis, (*b*) non-development of epiphyseal centre, and (*c*) fusion of epiphysis with diaphysis, but which of these is present in each particular case is not always evident. Of 19 and 16 instances respectively in girls aged 5 to 16 inclusive, not one epiphysis was present for the fourth, and only one for the third metatarsal (a girl aged 13 years and 7 months, where it was present on the right but not on the left side), although there were 13 and 7 epiphyses respectively in 34 and 30 instances in boys at these ages, suggesting that in females these phalanges are more vestigial than in the male.

MIDDLE PHALANX OF LITTLE TOE

Of 99 instances, including 30 females and 58 males aged 2 to 18, this epiphysis was found 4 times only, including 2 girls aged 2 years and 4 months and 3 years respectively, and a boy aged 12 years and 1 month. It is the exception rather than the rule for this epiphysis to be present at any age.

DISTAL PHALANX OF HALLUX

This epiphysis was present in a girl aged 2 years and 4 months and in a boy aged 1 year and 9 months.

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
13	5	2	3	2
14	0	6	0	6
15	5	5	0	3
16	6	11	0	8
17	4	11	0	0
18	4	6	1	0

Fusion was present in a girl aged 13 years and 7 months on both sides and in a boy aged 15. In the majority of girls aged 15 and of boys aged 17 fusion was complete. Union had not yet occurred on either side in a boy aged 16 years and 6 months, nor was it fused in a girl of 18.

DISTAL PHALANGES OF SECOND, THIRD AND FOURTH TOES

The youngest subject where these have appeared in the case of the second and third toes was aged 3 (sex unknown). In a girl aged 3 years and 11 months those for the third and fourth toes were present. They were likewise noted in a boy aged 5, whilst in a girl aged 6 they were present for the second and fourth toes. It was absent in all these digits in a girl aged 3 and a boy aged 8.

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
13	3 3 4	1 1 2	1 1 2	1 1 2
14	0 0 0	4 4 3	0 0 0	4 4 3
15	2 3 3	3 4 3	0 0 0	0 1 0
16	5 6 5	6 6 7	0 0 0	2 2 2
17	1 1 2	5 4 5	0 0 0	0 0 0
18	4 4 5	5 3 4	1 1 1	0 0 0

The earliest to fuse were in a girl aged 13 years and 9 months in each case on both sides, and in boys aged 15. The majority were fused in girls at the age of 13 and in boys at 15. Instances of non-fusion in the case of each digit were found in males at the age of 16 and in a female at 18.

DISTAL PHALANX OF LITTLE TOE

Age	Instances in girls	Instances in boys	Epiphyses in girls	Epiphyses in boys
3	2	1	1	1
4	0	1	0	0
5	0	3	0	1
6	0	1	0	0
7	1	2	1	2
8	0	2	0	1
10	0	3	0	2
11	2	2	0	0
13	4	2	1	0
14	0	3	0	0
15	2	5	0	0
16	6	6	0	1

The earliest centres to appear in each sex were aged 3. The oldest girl with an epiphysis was aged 13 years and 8 months and the oldest boy 16.

CHRONOLOGICAL ORDER OF APPEARANCE AND FUSION OF EPIPHYSES

Before birth:		
Both sexes	Appearance	Head of humerus, distal femur, proximal tibia, calcaneum, talus
Female	,,	Cuboid
During first year:		
Both sexes	Appearance	Hamate, capitate, head of femur, third cuneiform
Female	,,	Capitulum, distal radius, distal tibia, distal fibula
Male	,,	Cuboid
During second year:		
Both sexes	Appearance	Proximal phalanges of inner four fingers
Female	,,	First metacarpal, distal phalanges of thumb, middle and ring fingers, tarsal navicular, first and second cuneiforms
Male	,,	Capitulum, distal epiphysis of radius, distal fibula
At age of 2:		
Both sexes	Appearance	Inner four metacarpals, first metatarsal, proximal phalanges of toes, distal phalanx of hallux
Female	,,	Proximal phalanx of thumb, middle row of phalanges of fingers
Male	,,	First metacarpal, distal phalanx of thumb, and distal phalanx of index, first cuneiform
At age of 3:		
Female	Appearance	Patella, proximal fibula, second metatarsal, third metatarsal, middle phalanges of second, third and fourth toes, distal phalanges of third and fourth toes
Male	Appearance	Triquetrum, proximal phalanx of thumb, middle phalanges of middle and ring fingers, tarsal navicular, second cuneiform
At the age of 4:		
Both sexes	Appearance	Fourth metatarsal
Female	,,	Head of radius, fifth metatarsal
	Fusion	Greater tubercle to head of humerus
Male	Appearance	Lunate, middle phalanges of index and little fingers, distal phalanges of middle and ring fingers, second metatarsal, third metatarsal, middle phalanx of second toe
At the age of 5:		
Both sexes	Appearance	Navicular (carpal), multangulum majus, greater trochanter, distal phalanx of second toe
Female	,,	Medial epicondyle, distal ulna, lunate, triquetrum, multangulum minus, distal phalanx of index
Male	,,	Head of radius, distal phalanx of little finger, patella, proximal fibula, fifth metatarsal, middle phalanges of third and fourth toes, distal phalanges of third and fourth toes
	Fusion	Greater tubercle to head of humerus
At the age of 6:		
Male	Appearance	Medial epicondyle, distal ulna, multangulum minus
At the age of 7:		
Female	Appearance	Distal phalanx of little finger
	Fusion	Rami of ischium and pubis
At the age of 8:		
Both sexes	Appearance	Apophysis of calcaneus
Female	,,	Olecranon
At the age of 9:		
Female	Appearance	Trochlea, pisiform
Male	Fusion	Rami of ischium and pubis
At the age of 10:		
Male	Appearance	Trochlea, olecranon
At the age of 11:		
Female	Appearance	Lateral epicondyle
Male	,,	Pisiform

At the age of 12:		
Male	Appearance	Lateral epicondyle
At the age of 13:		
Female	Appearance	Proximal sesamoid of thumb
	Fusion	Lower conjoint epiphysis of humerus, distal phalanx of thumb, bodies ilium, ischium and pubis
Male	,,	Capitulum to trochlea and lateral epicondyle
At the age of 14:		
Female	Appearance	Acromion, iliac crest, lesser trochanter
	Fusion	Olecranon, upper radius, proximal phalanx of ring finger, distal phalanx of thumb, head of femur, greater trochanter, distal tibia and fibula, apophysis calcaneus, first metatarsal, proximal phalanges of toes
Male	Appearance	Proximal sesamoid of thumb, base of fifth metatarsal
At the age of 15:		
Both sexes	Appearance	Sesamoid of little finger
	Fusion	Distal phalanges of second, third and fourth toes
Female	Appearance	Sesamoid of index and little fingers
	Fusion	Medial epicondyle, first metacarpal, proximal phalanx of thumb, distal phalanges of inner four fingers, proximal tibia, outer four metatarsals, middle phalanx of second toe, distal phalanges of inner four toes
Male	Appearance	Acromion
	Fusion	Ilium, ischium and pubis
At the age of 16:		
Female	Appearance	Distal sesamoid of thumb, tuber ischii
	Fusion	Inner four metacarpals, proximal phalanges of index, middle and little fingers, middle phalanges of fingers
Male	,,	Lower conjoint epiphysis of humerus, medial epicondyle, olecranon, head of radius, distal phalanx of middle finger, apophysis of calcaneus
At the age of 17:		
Both sexes	Fusion	Acromion
Female	,,	Upper conjoint epiphysis of humerus, distal ulna, distal femur, proximal fibula
Male	Appearance	Distal sesamoid of thumb
	Fusion	First metacarpal, proximal phalanges of thumb and ring finger, middle phalanges, index, middle and ring fingers, distal phalanges of thumb, index, ring and little fingers, head of femur, greater trochanter, distal tibia and fibula, metatarsals, proximal phalanges of toes, middle phalanx of second toe, distal phalanx of hallux
At the age of 18:		
Female	Fusion	Distal radius
Male	,,	Inner four metacarpals, proximal phalanges of index, middle and little fingers, middle phalanges of little finger, proximal tibia
At the age of 19:		
Male	Appearance	Sesamoid of index, tuber ischii
	Fusion	Upper conjoint epiphysis of humerus, distal radius and ulna, distal femur, proximal fibula
At the age of 20:		
Both sexes	Fusion	Iliac crest
Male	,,	Tuber ischii
At the age of 21:		
Both sexes	Appearance	Clavicle
Female	Fusion	Tuber ischii
At the age of 22:		
Both sexes	Fusion	Clavicle

Table of Epiphyseal Appearances and Fusions

The following table takes into account only the instances noted by the author and the various authorities quoted. (*a*) Earliest appearance of centres in each sex. (*b*) Age at which majority of centres appear in each sex. (*c*) Oldest subjects in which centres have not yet appeared. (*d*) Earliest age at which fusion has occurred. (*e*) Age at which majority of epiphyses have fused. (*f*) Oldest subjects in which fusion has not yet taken place. The figures give the ages in years and months [years only in columns (*b*) and (*e*)]. B.B. denotes before birth.

	(*a*)		(*b*)		(*c*)		(*d*)		(*e*)		(*f*)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Clavicle	11	12	21	21	—	—	—	—	22	22	26 11	25
Inferior angle of scapula	17	—	—	—	—	—	—	—	—	—	—	—
Base of coracoid process	4 6	—	—	—	7 6	10 3	—	—	—	—	—	—
Angle of coracoid process	10 2	14	—	—	—	—	—	—	—	—	16	19
Tip of coracoid process	—	14 7	—	—	—	16	—	—	—	—	—	—
Distal epiphysis of acromion	13 10	14 11	14	15	—	—	—	—	17	17	16 1	19 2
Head of humerus	B.B.	B.B.	B.B.	B.B.	—	6	—	—	—	—	—	—
Greater tubercle of humerus	1 8	11	—	—	11	3 6	—	—	—	—	—	—
Union greater tubercle and head of humerus	—	—	—	—	—	—	—	—	4	5	6	9
Union of conjoint epiphysis	—	—	—	—	—	—	16 8	16	17	19	18	19 2
Lateral epicondyle	8 6	10 7	11	12	16	16	—	—	—	—	—	—
Capitulum	9	11	>1	1	—	6	—	—	—	—	—	—
Trochlea	7	8 9	9	10	16	16	—	—	—	—	—	—
Fusion of distal epiphyses of humerus	—	—	—	—	—	—	10	12	—	13	16	15
Fusion of conjoint epiphysis to shaft	—	—	—	—	—	—	13 4	14 7	13	16	16	16
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	15	—	—
Medial epicondyle	3 10	5 9	5	6	6	7	10	12	14	16	16	17 0
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	16	—	19 3
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	14	—	16	—
Olecranon epiphysis	6	7	8	10	10	—	13	14	14	16	16 0	17 6
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	14	—	15	—
Head of radius	3 4	4 3	5	5	6	8	13	14	14	16	16	20
Do. Davies and Parsons	2	—	—	—	—	—	—	—	—	—	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	14	—	18	—
Distal epiphysis of radius	9	1	>1	1	—	1 9	16 6	18 5	18	19	20 5	23
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	16	—	19	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	19	—	—	—

	(a)		(b)		(c)		(d)		(e)		(f)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Distal epiphysis of ulna	5	5	5	6	7	12	16 6	18 5	17	19	22	23
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	15 11	—	18	—	—
Do. Paterson	4	—	—	—	—	—	—	—	—	—	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	—	—	—	—
Do. Pryor (U.S.A.)	—	—	—	—	—	—	—	—	16	19	—	—
Styloid process of ulna	—	13 10	—	—	—	—	—	—	—	—	—	—
Do. Borovansky and Hnevkovsky (Prague)	—	5 10	—	—	—	—	—	—	—	—	—	—
Navicular	5	4 6	5	5	5 5	8	—	—	—	—	—	—
Do. Pryor (U.S.A.)	3 6	4 4	4	6	6 4	8 3	—	—	—	—	—	—
Lunate	2 7	1	5	4	3 5	6 11	—	—	—	—	—	—
Do. Pryor (U.S.A.)	—	—	3	5	6 3	—	—	—	—	—	—	—
Triquetrum	1 6	2	5	3	3	4	—	—	—	—	—	—
Do. Pryor (U S.A.)	—	1 9	2	—	—	5 5	—	—	—	—	—	—
Pisiform	8 6	7	9	11	10	14 7	—	—	—	—	—	—
Do. Pryor (U.S.A.)	7 7	—	—	—	10 7	—	—	—	—	—	—	—
Hamate	9	10	>1	>1	—	1 week	—	—	—	—	—	—
Do. Pryor (U.S.A.)	3	7	—	—	7	—	—	—	—	—	—	—
Capitate	9	10	>1	>1	—	1 week	—	—	—	—	—	—
Do. Pryor (U.S.A.)	4 days	2 days	—	—	3	7	—	—	—	—	—	—
Multangulum minus	3 5	4 6	5	6	4	8	—	—	—	—	—	—
Do. Pryor (U.S.A.)	—	—	4	6	6 7	8 3	—	—	—	—	—	—
Multangulum majus	3 5	5	5	5	3 5	8	—	—	—	—	—	—
Do. Pryor (U.S.A.)	—	4 1	—	7	6 7	8 10	—	—	—	—	—	—
First metacarpal	1 2	2 6	1	2	2 5	3	13	14	15	17	15	19 7
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	16	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	15	—	—	—
Second metacarpal	1 11	1	1	1	2 5	2	14 9	16	16	18	18	20 7
Do. Davies and Parsons	1 3	—	—	—	—	—	—	—	—	—	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	14	—	18	—
Third metacarpal	1 11	1	1	1	2 5	3	15	16	16	18	17	20 7
Do. Davies and Parsons	1 3	—	—	—	—	—	—	—	—	—	—	—
Do. Galstaun (Hindu girls)	—	—	—	—	—	—	14	—	14	—	18	—
Fourth metacarpal	1 10	1	2	2	2 5	3	15	16	16	18	17	19
Fifth metacarpal	1 5	1	2	3	2 5	3	15	16	16	18	17	19
Do. Galstaun	—	—	—	—	—	—	14	—	14	—	18	—
All metacarpals—Palmer	—	—	—	—	—	—	14 5	—	—	—	—	—
Proximal phalanx of thumb	1 11	3 10	1	3	2 5	2 10	13 8	14	15	17	15 6	19 11
Index finger	1 4	1	1	1	—	—	13 8	14	16	18	16	19 7
Middle finger	10	1	>1	>1	—	2	13 8	14	16	18	16	19
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	—	—	19 3

	(a)		(b)		(c)		(d)		(e)		(f)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Ring finger	10	1	>1	1	—	3	14	14	14	17	16	19
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	—	—	19 3
Little finger	1 10	1	1	1	1 6	3	13	14	16	18	16	19
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	—	—	19 3
Proximal sesamoids of thumb	11 5	14 5	13	14	12	15	—	—	—	—	—	—
Sesamoid of index finger	11 6	14	15	19	23	27	—	—	—	—	—	—
Middle finger	13 10	14 0	—	—	—	—	—	—	—	—	—	—
Ring finger	—	21	—	—	—	—	—	—	—	—	—	—
Little finger	13 10	14	15	18	23	27	—	—	—	—	—	—
Distal sesamoid of thumb	16 3	15	16	16	23	27	—	—	—	—	—	—
Middle phalanx of index finger	1 11	4	2	4	2 5	2	13 8	14	16	17	15	19
Middle finger	1 11	3	1	3	2 5	2	15	15 11	16	17	16	19
Ring finger	1 11	3	1	3	2 5	2 6	15	14	16	17	16	19
Little finger	2	4	2	4	3 5	2 6	15	14	16	17	15	19
Distal phalanx of thumb	10	1	1	2	1 10	2	13	14	13	17	15	19 7
Do. Sidhom and Derry (Egyptian)	—	—	—	—	—	—	—	—	—	15	—	—
Index finger	5	2	5	2	1 11	2	14 9	14	15	17	15	17
Middle finger	1 11	4	1	4	1 2	2	14	14	15	16	15	17
Ring finger	1 11	4	1	4	2 5	3 6	14	14	15	17	16	17
Little finger	4	5	7	5	1 11	2	15 6	14	15	17	15	17
Union of ilium, ischium and pubis	—	—	—	—	—	—	10 6	13	13	15	16 10	16 3
Union of rami of ischium and pubis	—	—	—	—	—	—	3 11	5 9	7	9	11	10
Ischic-pubic union (Davies and Parsons)	—	—	—	—	—	—	—	3	—	—	—	—
Iliac crest	14	15	14	16	14	—	17	—	20	20	21	21 7
Tuber ischii	13 5	13	16	19	—	—	—	—	21	20	24	21
Anterior superior iliac spine	13 5	—	—	—	17	—	—	—	—	—	—	—
Head of femur	10	6	>1	>1	—	9	14	14	14	17	16 10	20 2
Do. Borovansky and Hnevkovsky (Prague)	—	3 weeks	—	—	—	—	—	—	—	—	—	—
Do. Davies and Parsons	6	—	—	—	—	—	—	—	—	—	—	—
Greater trochanter	2	3 11	5	5	4	6	14	15	14	17	16 10	17
Do. Borovansky and Hnevkovsky (Prague)	—	3 5	—	—	—	—	—	—	—	—	—	—
Lesser trochanter	9	10 9	14	—	—	—	—	—	—	—	16 10	17
Distal epiphysis of femur	B.B.	B.B.	B.B.	B.B.	—	—	14	16	17	19	19	19
Do. Pryor (U.S.A.)	P.B.*	—	—	—	—	3 days	—	—	—	—	—	—
Patella	2 6	3 11	3	5	3 0	8	—	—	—	—	—	—
Do. Borovansky and Hnevkovsky (Prague)	—	3 7	—	—	—	—	—	—	—	—	—	—
Fabella	17	16 5	—	—	—	—	—	—	—	—	—	—

* Premature birth. 2 days after 8 months.

* Premature birth. 2 days after 8 months.

	(a)		(b)		(c)		(d)		(e)		(f)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Proximal epiphysis of tibia	B.B.	B.B.	B.B.	B.B.	—	—	14	16	15	18	19	19
Do. Pryor (U.S.A.)	P.B.*	—	—	—	25 days	—	—	—	—	—	—	—
Proximal epiphysis of fibula	3 11	3 4	3	5	4	5	14	16	17	19	18	19
Do. Paterson	2	—	—	—	—	—	—	—	—	—	—	—
Distal epiphysis of tibia	7	9	>1	—	—	—	13	15	14	17	16 4	18
Do. Borovansky and Hnevkovsky (Prague)	—	3	—	—	—	—	—	—	—	—	—	—
Distal epiphysis of fibula	11	9	>1	1	7	1 8	14	15	14	17	16 4	18
Apophysis of calcaneus	7	7 5	8	8	7 9	8 7	12 10	15	14	16	16	18
Do. Borovansky and Hnevkovsky (Prague)	—	6 2	—	—	—	—	—	—	—	—	—	—
Cuboid—Pryor (U.S.A.)	P.B.*	B.B.	B.B.	—	25 days	13 days	—	—	—	—	—	—
Tarsal navicular	1 3	2 6	1	3	3	5	—	—	—	—	—	—
First cuneiform	1 8	2 6	1	2	11	2 2	—	—	—	—	—	—
Do. Davies and Parsons	1 0	—	—	—	—	—	—	—	—	—	—	—
Second cuneiform	1 8	2	1	3	2 6	2	—	—	—	—	—	—
First metatarsal	2 6	2 6	2	2	2 7	3 6	14	15	14	17	18	18
Do Davies and Parsons	10	—	—	—	—	—	—	—	—	—	—	—
Sesamoids of hallux	13 4	13	—	—	11	8	—	—	—	—	—	—
Second metatarsal	2 6	4 6	3	4	2 7	3	14	15	15	17	18	17
Third metatarsal	2 6	4 6	3	4	2 7	3	14	15	15	17	18	17
Fourth metatarsal	3 11	4 6	4	4	3	4 6	14	15	15	17	18	18
Fifth metatarsal (head)	3 11	4 6	4	5	3	4 6	14	15	15	17	18	18
Fifth metatarsal (base)	12	13	—	14	—	—	—	—	—	—	13 7	16
Do. Borovansky and Hnevkovsky (Prague)	—	11 7	—	—	—	—	—	—	—	—	—	—
Proximal phalanx of hallux	2 6	2 6	2	2	2 4	2 6	14	15	14	17	18	17
Do. Davies and Parsons	10	—	—	—	—	—	—	—	—	—	—	—
Proximal phalanx of second toe	2 4	2 2	2	2	2 7	2 6	14	15	14	17	18	17
Third toe	2 4	2 2	2	2	2 7	2 6	14	15	14	17	18	17
Fourth toe	2 4	2 2	2	2	2 7	2 6	14	15	14	17	18	17
Fifth toe	2 4	2 2	2	2	2 7	2 6	14	15	14	17	18	18
Middle phalanx of second toe	2 4	3	3	4	3	8 7	12	15	15	17	18	16
Third toe	2 4	3	3	5	—	—	13 7	—	—	—	18	16
Fourth toe	2 4	5 2	3	5	—	—	13 7	—	—	—	4	16
Fifth toe	2 4	12 1	—	—	—	—	13 7	—	—	—	—	—
Distal phalanx of hallux	2 7	1 9	2	2	—	2 6	13 7	15	15	17	18	16 6
Second toe	6	5	5	5	3	8	13 9	15	15	15	18	16
Third toe	3 11	5	3	5	3	8	13 9	15	15	15	18	16
Fourth toe	3 11	5	3	5	3	8	13 9	15	15	15	18	16
Fifth toe	3	3	—	—	—	—	—	—	—	—	13 8	16

* Premature birth. 2 days after 8 months.

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EXPLANATION OF PLATES I AND II

Plate I (figs. 1–5).

Fig. 1. Boy, age 14 years 7 months. Demonstrating (*a*) epiphyses at angle of coracoid, (*b*) tip of coracoid, (*c*) acromion process, (*d*) fused head and greater tubercle of humerus.

Fig. 2. Male, age 6 years and 11 months. Multangulum majus well marked on left, but completely absent on the right; lunate just appeared on right but no trace on left.

Fig. 3. Same hands as fig. 4. Note two centres for lunate on left side, one dorsal to other.

Fig. 4. Female, age 6. Note two centres for lunate on left side.

Fig. 5. Sesamoids at heads of all metacarpals. Two sesamoids over fifth.

Plate II (figs. 6–10).

Fig. 6. Age 21. Sesamoids at heads of first, second, third and fifth metacarpals. Large sesamoid over *centre* of third metacarpal.

Fig. 7. Male, age 18. Epiphyses along perineal margin at apex of perineal triangle.

Fig. 8. Female, age 14. Epiphysis for anterior superior iliac spine.

Fig. 9. Female, age 17. Epiphysis for anterior superior iliac spine.

Fig. 10. Female, aged 2 years and 3 months. Two centres present for first cuneiform.

Fig. 1.

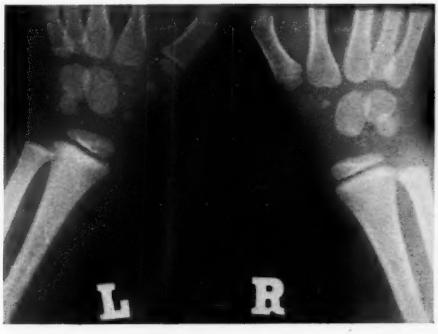

Fig. 2.

Fig. 3.

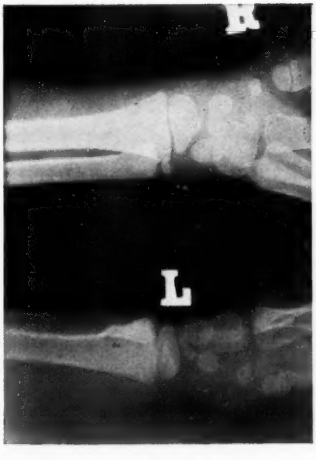

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

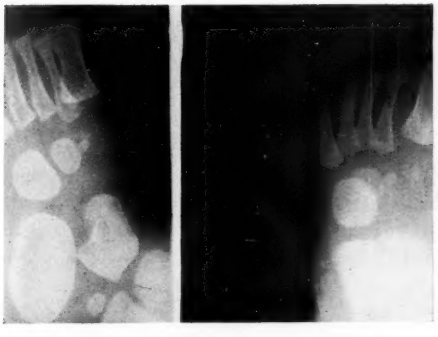

Fig. 10.

AN UNUSUAL FORM OF BRACHYPHALANGY AND SYNDACTYLY, WITH DOUBLE PROXIMAL PHALANX IN THE MIDDLE FINGERS

By E. A. COCKAYNE, D.M., F.R.C.P.

R.J., the boy with the abnormality, was brought to the Hospital for Sick Children, Great Ormond Street, in October, 1931. He was then aged 8 months, the only child of first cousins, who are English and live at Watford. His mother says that as far as she knows no similar deformity has been present in any other member of the family. The boy appears to be of normal intelligence, but is small for his age, weighing 10 lb. 5 oz. at 13 months, and has a harsh systolic murmur, which is loudest over the lower part of the sternum and is probably due to a patent interventricular septum.

In each hand the index finger is very short and sharply bent in the middle so that the distal end points towards the middle finger. There is complete syndactyly of the middle and ring fingers of each hand, but the union is confined to the soft tissues and the nails are not joined together, and each middle finger is reduced in length so that it is shorter than the ring finger. A skiagram taken in October shows that in both index fingers the middle phalanx is represented by a minute spherical bone, and the proximal phalanx is very small, misshapen, and much shortened in the right hand and shortened to a less extent in the left. In the middle finger of the right hand the proximal phalanx is represented by five small bones, of which three lie in the long axis of the finger on its radial side, the middle one being considerably the largest, and the other two lie close together at the same level on its ulnar side. In the left hand the proximal phalanx of the middle finger is represented by two small bones, one of which lies on its radial side in the same position as the three bones in the middle finger of the opposite hand, and the other lies on its ulnar side. These bones are all very small, and even combined their mass would be much less than that of a normal proximal phalanx. The proximal phalanx of the left ring finger is considerably shorter than that of the right one, which appears to be of normal length, and the middle phalanx of both little fingers is reduced in length. There is a bifurcation of the ungual phalanx of the index finger of the left hand, an anomaly mentioned by Cunningham, and a similar bifurcation appears to be present in the other index, but the phalanx is very slender.

In the feet there is no syndactyly and no visible deformity, but the skiagrams show that the middle phalanx of both second toes is absent. Only two bones are present in each little toe, but this is probably normal, as the proximal and middle phalanges are often fused.

Skiagrams taken on 25 February, 1932, when the boy was 13 months old, show the arrangement of the abnormal bones more clearly. In the right hand the proximal phalanx of the middle finger appears to be replaced by three bones on the radial side, the largest of which articulates with the middle phalanx and three on the ulnar side. The latter group is very little further away from the metacarpal than the most proximal of the radial group and much nearer to it than the two others belonging to the radial group. In the left hand there are two groups of very small bones replacing the proximal phalanx of the middle finger, but it is difficult to be sure whether there are three in each group or only two, though I think there are three. The position of those on the ulnar side corresponds in the two hands, but on the radial side the group in the left hand is intermediate in position between the two nearest to the middle phalanx and the one nearest to the metacarpal in the right hand.

I have never met this form of brachyphalangy before, nor have I seen any published description of it. In some respects it resembles the condition described by Drinkwater under the title "Hereditary Abnormal Segmentation of the Index and Middle Fingers." In this there is remarkable reduction in the length of the index and middle fingers and the middle phalanx of the index is aborted. In the index there is a bone of approximately the same length as the proximal phalanx lying between it and the head of the second metacarpal and becoming fused with the proximal phalanx in adult life, and in the middle finger a triangular bone is interposed on the radial side between the proximal phalanx and the head of the third metacarpal and becomes fused with the phalanx in later life. Drinkwater regards these bones as extra bones arising from an abnormal division of the primitive mesenchyme. Though different in position they may be compared with the extra bones in the position of the proximal phalanx of the middle fingers of my patient. These are looked upon by Dr Bertram Shires, to whom I am indebted for the skiagrams, as extra bones, and he thinks that there is a double phalanx. If so the cause is probably another kind of abnormal division of the mesenchyme in early embryonic life. Drinkwater's patients had no syndactyly, the feet showed ordinary brachydactyly, the abnormality was inherited as a simple dominant, and so the condition differed in all these three respects from that present in my patient.

Olaf Thomsen has described as the Vordingborg type a syndactyly of the middle and ring fingers with partial or complete doubling of the middle fingers. In some cases the middle phalanx and in others the third metacarpal is branched and all the parts distal to the bifurcation are doubled. Sometimes, however, instead of a simple branching of the metacarpal there is an isolated bone opposite the base of the branched phalanx or the head of the single metacarpal and this bone probably represents part of an extra metacarpal. The condition agrees with that seen in my patient in the association of syndactyly with reduplication of parts, but the reduplication is much more complete and different in character. It differs in the absence of brachyphalangy and in its mode of

Left

Right

Left

Right

inheritance. Males are affected more often than females, and up to the present time it has been transmitted only by males. It is evidently a dominant.

Though differing in minor points the defects in the hands and feet of this boy are in the main symmetrical and this bilateral symmetry makes it almost certain that the abnormality is genetic in origin. It is indeed common to find much greater asymmetry in inherited osseous defects of the extremities. A number of distinct forms of brachyphalangy and of syndactyly occurring either alone or in combination have been described, but with one exception all those with which I am acquainted are autosomal dominants. The one exception is the form of syndactyly described by Schofield, which is transmitted by males only to all their sons and is probably due to a gene in the *Y*-chromosome. Since the parents of this boy are normal the defect cannot be dominant unless it arose as a new mutation, but it may be recessive, and the fact that the parents are first cousins makes this very probable.

For whereas amongst the general population the percentage of marriages between first cousins is on the average 0·5–1 per cent., in the case of those that give rise to one or more children with a recessive defect the percentage rises from 17 in the case of a relatively common one, such as albinism, to 50 or more, and the rarer the defect the higher is the percentage of first cousin marriages giving rise to it. Thus the high percentage of first cousin marriages in the parents is the most reliable indication that a defect is recessive. Though no safe deduction can be drawn from a single case, we have here a rare defect apparently of genetic origin in the child of first cousins, and the suspicion at once arises that it may be recessive. The case is therefore worth recording, for it is only by publishing descriptions of single cases with full family histories that the mode of inheritance of rare recessive abnormalities can be proved. No single observer can hope to see enough cases himself, but if single cases are published sufficient data can be collected from the literature in course of time, and I hope this short paper will lead to the publication of other cases of the same kind.

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A CASE OF ENLARGED PARIETAL FORAMINA ASSOCIATED WITH METOPISM AND IRREGULAR SYNOSTOSIS OF THE CORONAL SUTURE

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Greig, who has been one of the principal writers on the subject of enlarged parietal foramina, has stated that the condition is sufficiently rare to make it desirable that every case should be recorded. It was felt therefore that an account of this case should be published, more especially as the skull presents in addition the unusual feature of persistence of the metopic suture with irregular synostosis of the coronal suture. This opportunity was also considered to be a suitable one to place on record the incidence of parietal foramina in the series of over 310 Maori and Moriori skulls which the Department possesses.

INCIDENCE OF FORAMINA IN MAORI AND MORIORI SKULLS

By Moriori skulls is to be understood skulls obtained from the Chatham Islands. These numbered only 38 in the total of over 310 skulls and calvaria examined. The presence of a parietal foramen was not accepted unless a probe could be passed completely through into the interior of the skull. Doubtful cases were rejected, bringing the total number from which data were collected to 310, and the results of the examination are as follows:

Total number presenting	both right and left foramina	91 = 29 %
,, ,,	a right foramen alone	72 = 23 %
,, ,,	a left foramen alone	63 = 20 %
,, ,,	a sagittal foramen	8 = 2·6 %
Hence the number in which the foramen was represented		234 = 75·5 %

Comparing these findings with those previously recorded by other observers the incidence of the foramen is slightly higher than any hitherto given. For example, Greig ((7), p. 640) in a series of 670 skulls and calvaria found that the foramen was present in 70·29 per cent. of cases. His figures were:

Both foramina present in	45·6 %	Left one present in	12·0 %
Right one present in	12·9 %	Sagittal one present in	5·3 %

Cave ((4), p. 173) in recording his findings from a series of 250 skulls states that in 100 ancient Egyptian ones the foramen was represented in 67 per cent.

and was bilateral in 30 per cent. In the remaining 150 which were modern skulls it was present in 61 per cent. and bilateral in 32 per cent. In a summarised total of 4228 skulls and calvaria described by Le Double, Paterson and Lovegrove, Maciesza, Gruber, and Greig and published by Greig ((7), p. 641) the foramen was present in 62·39 per cent. of cases. Moreover in this large series it was observed that the right was present nearly twice as often as was the left, a finding not supported in the smaller amount of material examined by Greig alone or in the present series of 310 cases. Adding to the previous summary the 250 cases described by Cave and the 310 recorded here the incidence of the parietal foramen in the total of 4788 skulls and calvaria is 63 per cent.

In considering these recorded findings it appears that as far as the data collected will allow of a definite conclusion being drawn the incidence of foramina parietalia is remarkably constant whatever the origin of the skulls examined or the age period to which they belong, be they ancient or modern, Egyptian or Maori. The foramen appears to be quite a usual feature of the human skull.

ENLARGED PARIETAL FORAMINA

Despite the large number of skulls which have been examined for parietal foramina and their high rate of incidence, it is rather remarkable that the recorded instances of enlarged foramina are distinctly rare. Thus in 1919, Pamperl ((8), p. 172) was able to collect only 36 cases from the literature. To these have been added since that date three cases by Greig (7), two by Cave (4), two by Boyd (3), and one by Stibbe (9), thus making with the case recorded here a total of 46. This total includes a case described by Greig in 1917 ((6), p. 205) and omitted by Pamperl from his summary.

The present case consists of a skull recently acquired by this Department. Nothing is known of its history beyond the fact that it was purchased from a dealer by a student as part of a half set of bones. An examination of the remaining bones of the set revealed no unusual features. The skull is small and light, being within the microcephalic range with a capacity—determined by the water method—of 1280 c.c. It is also markedly brachycephalic and appears to be from an adult female. Dentition is incomplete, no third molars having erupted.

The parietal foramina are bilateral, of approximately equal size, somewhat oval in shape with the long axis passing at right angles to the line of the sagittal suture. Each is situated in relation to the postero-superior angle of the parietal bone, and between the two the sagittal suture is synostosed for 30 mm. of its length. The left parietal bone is depressed relatively to the right and the original suture line remains as the line of union of the two planes and is curved with the concavity to the left. The edge of each foramen is smoothly bevelled at the

expense of the outer table with a resultant difference in the internal and external measurements of the foramina. These measurements are:

Right foramen:	Coronal diameter	8 mm. externally. 7 mm. internally.
	Sagittal diameter	5 mm. externally. 4 mm. internally.
Left foramen:	Coronal diameter	7 mm. externally. 6 mm. internally.
	Sagittal diameter	7 mm. externally. 4 mm. internally.

The posterior border of the right foramen is somewhat irregular, especially at its medial end, due to several narrow grooves running across its edge. Of these grooves one, the largest, definitely notches the external table at the margin of the foramen and internally is continuous with one of the large vascular grooves on the parietal bone. This notch is well shown in fig. 3. Externally with the one exception just mentioned there is no grooving, suggesting the passage of anastomosing vessels through the foramen, but internally a wide and definite groove connects the lateral angle of each foramen with converging grooves formed by the meningeal vessels. In addition other meningeal channels appear to commence separately at the posterior border of each foramen, while from the medial angle of the left foramen a wide groove runs into the sagittal sulcus which is itself well marked in this region. This grooving is illustrated by fig. 4. It would appear then that in this case there has been a rich vascular communication through each foramen between the meningeal and the scalp vessels.

Situated just medial to the inner margin of the right foramen between it and the sagittal suture are two minute accessory foramina communicating separately with the interior of the skull. These foramina are on the line of the parietal suture concerning which so many references are found in the literature on parietal bone development.

As already indicated the skull possesses in addition an interesting condition of the sutures:

The *lambdoid suture* is completely present with large denticulations especially marked on the left side.

The *masto-occipital suture* is open on each side.

The *sagittal suture* is clearly marked externally, excepting for a length of approximately 30 mm. where between the two parietal foramina it is almost completely synostosed and is represented by a curved line with the concavity of the curve directed to the left as seen in fig. 2. Internally it is open anteriorly but gradually becomes obliterated along the middle third of its course, and in the posterior third is only faintly discernible.

The *metopic suture* is open externally, but endocranially is undergoing synostosis from before back.

The *coronal suture* is entirely obliterated on the left side with no remaining

Fig. 1. Lateral view showing general shape of skull and obliteration of coronal suture.

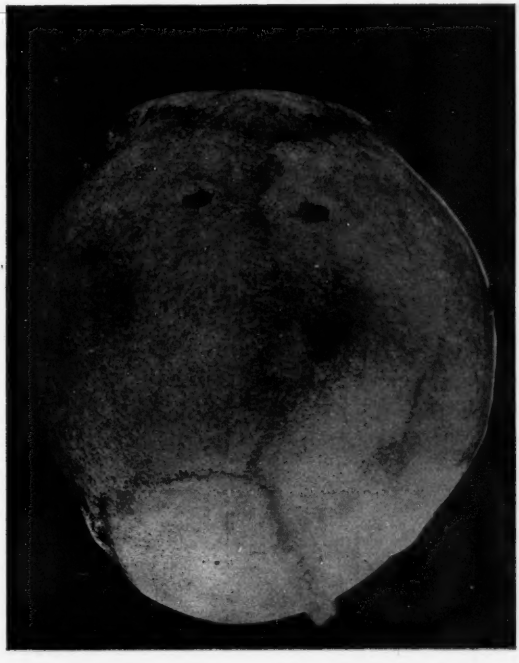

Fig. 2. Norma verticalis, illustrating asymmetry of vertex, metopic suture, parietal foramina and obliteration of left half of coronal suture.

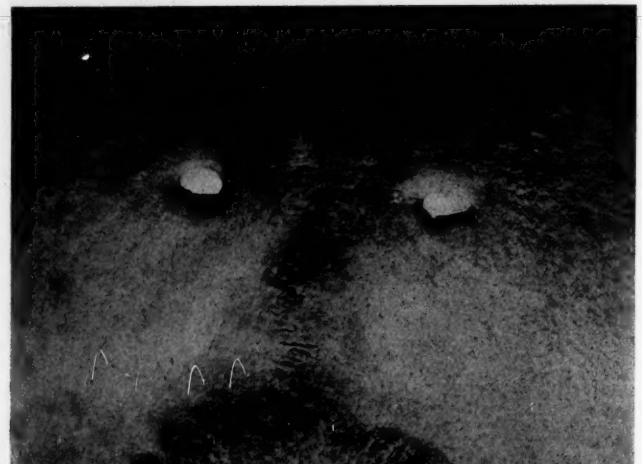

Fig. 3. External view of the parietal foramina. The notch on the posterior border of the right foramen is well shown.

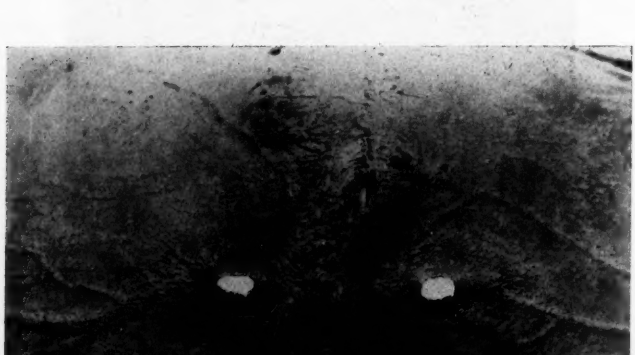

Fig. 4. Internal view of the parietal foramina illustrating the vascular grooves.

trace internally or externally. So complete indeed is the synostosis that the left frontal and parietal bones appear to be a single bone. On the right side there is no trace of the suture on the endocranial surface, but externally it is clearly defined from the sagittal suture to the Pterion where the terminal 12 mm. of the suture is obliterated and the bone is of parchment thinness. This thinness is due to absorption of the outer table of the skull with the formation of a groove which passing vertically downwards is continuous with a narrower groove extending as far as the level of the upper border of the zygomatic arch and occupying approximately the line of the middle deep temporal artery ascending from the Pterygoid region. Similarly at the left pterion the bone is of tissue paper thinness, but here this is due to complete absorption of the inner table and diploe along the line of a groove formed by the anterior division of the middle meningeal vessels and leading into a short bony canal for the same vessels extending upwards for 3 mm. from the level of the posterior free border of the small wing of the sphenoid.

The irregularity in suture closure has resulted in a marked asymmetry of the skull. This is well seen in the vertex (fig. 2), the long axis of which is seen to pass through the right frontal eminence. The asymmetry is not, however, confined to the vertex but is seen also in the fossae at the base. Thus the left posterior and middle fossae are deeper than those on the right, with a corresponding depression of condylar process and temporal bone on that side. The right anterior fossa is broader than the left. There is no demonstrable difference in the size of corresponding basal foramina on the two sides. The facial portion of the skull is also asymmetrical as seen in the palate, but details of this or of the alveolar process in either jaw cannot be given owing to the fact that these processes have been built up with plaster. The right ascending ramus of the mandible is considerably broader at its widest part (28 mm.) than is the left one (24 mm.). In addition, probably owing to the lower position of the left glenoid fossa, the mandibular neck on this side is shortened by a lateral convexity. In this way the asymmetry of the base is compensated for.

DISCUSSION

The various forms of parietal foramina, be they unilateral, bilateral, single median, or duplicated on one or both sides, have been attributed by Broca to various types of ossification replacing the sagittal fontanelle. At times a short transverse parietal suture is found on one or both sides in this region. As already stated the presence of parietal foramina may be considered as normal, but when they are enlarged it may be assumed that some disturbance in bone formation and growth has occurred. The condition comes therefore under a similar category to that of congenital thinning of the parietal bone. It is interesting to note in this connection, however, that in none of the five cases of parietal thinning in the Museum of this Department is there any abnormality of the parietal foramina. The occurrence of metopism associated with irregular

synostosis of the coronal suture in the case now recorded supports Greig's contention that general body growth disturbance and local dysplasia are frequent accompaniments of enlargement of the parietal foramina. Attention must, however, be directed to the very definite vascular grooving on the inner table of each bone in relation to the foramen. Boyd ((3), p. 110) writing on the subject of emissary foramina states that in connection with the recorded cases of enlarged parietal foramina a large vascular groove on the inner table has seldom been seen, and he cites as an exception to this the case of an Australian skull described by him and presenting a groove passing backwards between the foramen and the right transverse sulcus. He supports the view that enlargement is not due to vascular communication between the meningeal and scalp vessels but rather to primary defective ossification.

What the determining factor is in causing defective bone formation in this particular area and often in symmetrical bilateral positions has still to be determined. Although a normal parietal foramen might be explained as due to arrested ossification round a vessel or vessels it is inconceivable that the enlarged type of foramen could be due solely to this cause. It would seem that we shall have to await further details regarding the factors which control the normal growth of bone in general, and also the factors which influence the closure of the sutures on the vertex of the skull before any satisfactory attempt at explanation of these apparent anomalies of development could be made.

In conclusion I wish to express my thanks to Prof. Gowland for permission to record this case, for the opportunity of examining the Departmental collection of Maori and Moriori skulls, and for his advice and assistance in the arrangement of this paper.

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ANATOMICAL NOTES

A CASE OF DUPLICATION OF THE INTERNAL CUNEIFORM BONE OF THE FOOT (*CUNEIFORME BIPARTITUM*)

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A JOCKEY, aged 34, presented himself with a wound on the inner side of the right foot sustained a week previously when he was thrown from his sulky. A radiogram showed that in addition to a fracture of the scaphoid, there was an unusual appearance in the region of the internal cuneiform. A series of stereoscopic radiograms of both feet were then taken, and it was found that there was a bilateral condition of duplication of the internal cuneiform.

Figs. 1 and 2 show the radiological appearance of the left foot as seen from the dorsal aspect with the foot in an everted position. In fig. 2 the bones are outlined, and it can be seen that the division between the two elements is oblique, one being dorsal and lateral, the other plantar and medial. Both elements articulate with the scaphoid and with the base of the first metatarsal. The condition was not revealed by inspection and palpation, as the plantar element is in true alignment with the medial border of the foot.

The literature shows considerable difference of opinion as to the frequency of this condition.

Cases of partial division seem to be fairly common, and several examples were found in the osteological collection here.

Two of these are shown in figs. 3 and 4. The usual condition is the presence of a transverse groove on the distal articular surface. This is well seen in fig. 3. The specimen illustrated in fig. 4 showed grooves on both proximal and distal surfaces, and in addition a general narrowing is observed indicating a division into dorsal and plantar portions. In cases of complete division the bone is stated to be divided transversely into two elements, i.e. cuneiforme 1, plantare and cuneiforme 1, dorsale of Pfitzner.

Dwight (1907)(3) states that although he had been searching carefully for years he had never seen a case of complete division in the dissecting room, though he had seen it in a radiogram of a child's foot.

Poirier and Charpy (1911)(7) on the contrary mention several authorities who have seen the bone in two parts articulating with one another by an arthrodial articulation. They further quote Pfitzner as having encountered in a series of 450 feet 4 cases of complete division and 6 cases of partial division. The plantar segment is regarded by Volkow as a sesamoid bone and by Pfitzner as the remains of a marginal ray or supernumerary sixth toe.

It is stated that two centres of ossification instead of the usual single one have been occasionally observed.

According to Koehler(5) the condition when seen radiologically is frequently bilateral, and in some cases examination at a later date shows partial or complete union to have occurred.

Fig. 1. Left foot, untouched.

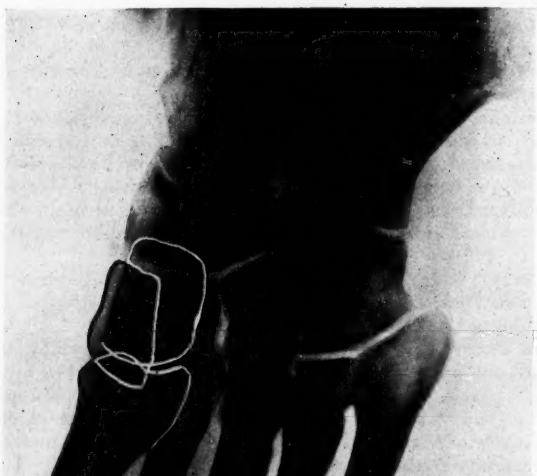

Fig. 2. Left foot. Bones outlined.

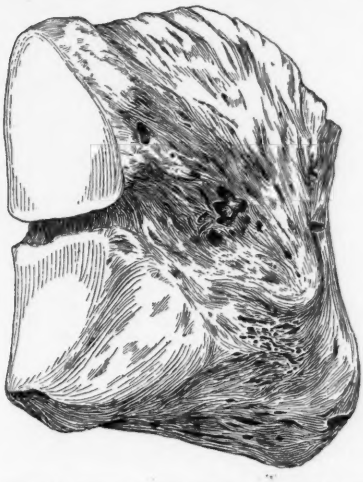

Fig. 3. Right internal cuneiform showing distal surface.

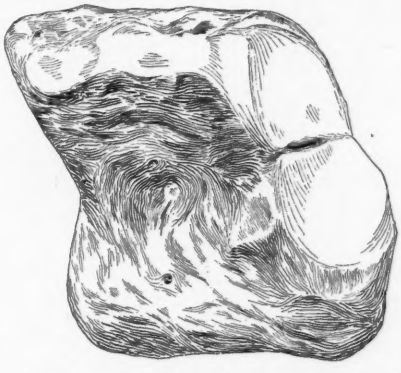

Fig. 4. Left internal cuneiform showing proximal surface.

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SOME REMARKS ON THE ACTION OF THE SACROLUMBALIS DURING STANDING

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I think I am right in saying that a good deal of uncertainty still exists in the minds of many persons concerning the exact action of the sacrolumbalis during the ordinary standing "at ease" and the military standing "at attention" positions respectively, and I therefore hope that the remarks below will prove of some interest.

A. *The ordinary standing "at ease" position*

In this position the lumbar vertebrae have to be fixed so that movements of flexion and extension in both lateral and antero-posterior planes are prevented. As regards the former, this is done by a moderate amount of contraction in three muscles, namely the sacrospinalis, quadratus lumborum and the psoas. The synergic action thereof, equal on both lateral halves of the body, forms a tripod for fixation of the lumbar spine to prevent any lateral movement. And just because it is a tripod, this diminishes the necessity for anything more than a quite moderate degree of contraction in each of its three integral muscles. And in the position under consideration, palpation will reveal only a very small amount of contraction in the sacrospinalis, unless of course the subject tries to stand on one leg or essays to bend forward or backward.

As regards the maintenance of a constant amount of antero-posterior concavity in the lumbar vertebrae, this is effected by ligamentous and not by muscular action. As a necessary initial step, the pelvis must be immobilised, and this is done by many of the muscles that pass from it to the thighs, not the least important of these being the hamstrings. These muscles, as is well known, are amongst the most inextensible in the body, and I think that this is simply due to a wise provision of Nature that such inextensibility may to a very large extent replace the necessity for tonic contraction in the muscles in question and thus materially delay the onset of fatigue in the standing position.

The immobility of the pelvis having fixed the fifth lumbar vertebra, the lumbar spine, under the influence of the superimposed weight of the head and thorax, becomes extended on itself until any further increase in its concavity is arrested by the anterior common lumbar ligaments being put upon the stretch. These ligaments are very strong and inextensible and they are fully capable, under ordinary circumstances, of resisting any excess of increase of lumbar concavity during prolonged periods of standing without fatigue or pain ensuing. Any additional help that may be afforded to these ligaments by the tonus of the anterior abdominal muscles is so slight as to be almost negligible.

From the above it can be seen that the sacrospinalis, in the standing " at ease" position, acts chiefly as a lateral steadier of the lumbar region and has hardly any action as an extensor of these bones.

The above does not, of course, apply to those subjects who on standing "at ease" cause the lumbar vertebrae to be lordosed, as is of fairly frequent occurrence in girls. In this case the sacrospinalis contracts more than in unlordosed subjects, but not as much as in the military "attention" position (see below). The hamstrings act in the same way, and the result of their contraction not being very great in the above lordosed position, the pelvis is allowed to rotate so that its posterior half is elevated. The nett result of the lordosed position will be that the anterior common lumbar ligaments will be more stretched than before, as they will have to bear the increased

force from the sacrospinalis in addition to the weight of the thorax and head. They are quite capable, under ordinary circumstances, of withstanding such extra force elongating them, but pain and strain will ensue easier unless the position be abandoned at intervals. This explains, I think, why persons who adopt this lordosed position generally get tired relatively much quicker when standing than those who really stand "at ease."

B. *The military standing "at attention" position*

In this position the subject makes efforts to straighten out his whole spinal column and make himself as tall as possible[1]. This is effected as follows: (1) the dorsal erector spinae contracts together with some of the other muscles of the thoracic wall: this if unopposed would elevate the ribs and extend the dorsal spine backwards; (2) the hamstrings and other pelvo-crural muscles contract in order to fix the pelvis more effectually; this if unopposed would rotate the pelvis so that its posterior portion would descend; (3) the sacrospinalis contracts powerfully, and this if unopposed would extend the lumbar vertebrae (thereby increasing their concavity), rotate the pelvis in the direction opposite to the one mentioned under (2) and assist the dorsal extension mentioned under (1); (4) the anterior abdominal muscles contract, and this if unopposed would pull the anterior part of the ribs down and elevate the anterior half of the pelvis.

The nett result of all these muscular actions, however, when combined in correct proportion, results in the maintenance of the posture with a straightened spine. This is brought about by the pelvis hardly moving at all, the thoracic cage becoming a fixed entity, capable of movement only *en masse* on a hinge in the dorso-lumbar junction; the sacrospinalis forms a bowstring between the sacrum and the lowest dorsal vertebra, and as it is prevented from approximating these two bony points, a great part of its energy is spent in trying to convert itself from a curved line (with its concavity backwards) into a straight one. Thereby it produces a diminution of the lumbar concavity, or in other words it acts as a flexor of these bones and not an extensor. In this flexor effect it is assisted by the contraction of the anterior abdominal muscles, which by attempting to approximate the lower ribs to the symphysis, press the anterior portions of the lumbar vertebra together, i.e. straighten out the lumbar spine by promoting flexion in them. In this position, therefore, the action of the anterior abdominal muscles is not entirely antagonistic to the sacrospinalis, but partly synergic. Under other circumstances these two muscular masses are always antagonistic; this is clinically shown by the facts that paralysis of the anterior abdominal muscles or too great strength in the sacrospinalis can induce lordosis, the opposite conditions respectively causing kyphosis. (*Vide* the so often reproduced illustration no. 98 in Duchenne, *Physiologie der Bewegungen*, 1885, p. 572.)

The sensation of intense work in the sacrolumbalis during the maintenance of the above position is, I think, due to this muscle being in a state approaching maximum activity while in a state of being greatly elongated. The whole state of affairs of this muscle in the position under consideration is analogous to that in the posterior cervical muscles during the maintenance of this posture. These muscles, which if unopposed would extend the cervical vertebrae, are prevented from doing so and thus expend their energy in straightening out the cervical concavity as viewed from behind.

[1] It must here be pointed out that all countries do not have absolutely the same ideas concerning what constitutes the military standing "at attention" position, but the above definition is the one most usually adopted in physical and military drill in this as well as many other countries. It must also be pointed out that the words of command "stretch your back" and "make yourself as tall as possible" respectively do not always produce the same result, as the first may cause the subject to become shorter and the latter makes him increase his vertebral length (Haglund, *Arch. f. Orthop. u. Unfall. Chir.* 1910, vol. XXVII, pp. 95–100).

BILATERAL ABSENCE OF TRAPEZIUS

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VARIATIONS in the trapezius are well recognised conditions (1,2), and complete absence of the muscle on one side has been observed in some cases (3), but no mention in the literature can be found of bilateral absence of the trapezius. Clinical cases of extensive bilateral defect are reported by Erb (4) and Voltz (5), and Grauhan (6) reports a case where the lower part of the trapezius (the dorsal attachment) was missing on both sides. More recently Schulze-Gocht (7) in a clinical study reported twelve people in whom the trapezius was absent or defective, nine on the left side and three on the right. No evidence of the underlying etiology could be discovered in these cases. The occurrence of defective or non-development of this muscle in association with the presence of a cervical rib has been noticed by some clinical observers, but no clear evidence as to the existence of any relationship has yet been forthcoming.

In view of these facts, an example of complete bilateral absence of the trapezius, which occurred in one of the dissecting-room subjects last year, has been considered worthy of a short record. The subject was a male aged 70 years who had complained of intermittent attacks of cervical muscular spasm for over thirty years. There was a history of an operation at Bristol many years ago, but no details could be obtained as to the nature of this operation. A report on his clinical condition shortly before he died states that there was spasm of the left sterno-mastoid with clonic movements of the left facial and left shoulder muscles. The chin was raised and tilted to the right. There was a short vertical scar about two to three inches long immediately to the left of the dorsal spines, extending from the level of the sixth cervical to the first dorsal. Death was due to myocarditis and arteriosclerosis with subsequent cardiac muscle failure.

On dissection, the trapezius was found to be completely absent on both sides of the body. A tendinous insertion of the deep fascia of the posterior shoulder region into the spine of the scapula could be isolated on the right side. The sterno-mastoid appeared normal on the left side, but was very weakly developed on the right. The rhomboids were present and were more prominently developed than usual. No other muscular abnormalities were noticed in the course of dissection. The spinal accessory on the left side was normal in size and appearance, and ended in the substance of the sterno-mastoid muscle. On the right side the spinal accessory nerve, after a short extra-cranial course of half to three-quarters of an inch, terminated in a bulbous enlargement, from which a few twigs passed to the feebly developed sterno-mastoid. Microscopically this bulb showed the typical appearance of a fibro-neuroma.

Though this case is recorded as an example of bilateral absence of the trapezius, it cannot be accepted unquestionably as a congenital condition. The presence of the bulbous termination of the right spinal accessory nerve, together with the absence of the trapezius and feeble development of the sterno-mastoid on the corresponding side, suggest the possibility of a nerve lesion following some injury in early life, possibly at birth. This suggestion, however, still leaves the associated absence of the trapezius on the left side unexplained, for the length and position of the scar

on this side place out of court any question of serious damage to the muscle at the time of operation.

I am indebted to Dr Luxton, late Resident Medical Officer of Hope Hospital, Salford, for the clinical records of this case.

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DESCRIPTION OF THE SKULL OF A GIRL OF 17

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Introduction

The skeleton of which the skull described forms a part was obtained from a dissecting room female subject who was known to be 17 years of age and imbecile.

As the opportunities for examining adolescent skeletons are comparatively rare it was thought desirable to record the characters, metrical and non-metrical, of the skull, and on a later occasion to publish an account of the remainder of the skeleton.

Measurements were made with Flowers' Craniometer and Parson's Rigid Bar.

Dioptographic tracings of the skull, viewed from three different aspects, are shown. The orientation is such that in each case the Frankfort plane is parallel to the true horizontal or vertical. Contour lines, 1 cm. apart, have been drawn parallel to a fixed base to facilitate comparison with skull types.

Characters relating to age and sex

1. *Sutures.* The term "closure" has been used variously. Some writers mean by it firm interlocking of two bones along a suture, with reduction of fibrous tissue to a minimum; others, the conversion of a suture into a synostosis. It is used here in the latter sense. In the vault, all the sutures *including the Metopic* are firmly interlocked but quite distinct. The petro-squamosal suture is open in its anterior two-thirds. Synosteal change is beginning around some of the Wormian bones in the lambdoidal suture and in the posterior third of the petrosquamosal suture. In the base, spheno-occipital union is almost complete. The occipito-mastoid suture is interlocked posteriorly but open on the floor of the sigmoid sulcus.

2. Muscular and ligamentous markings are slight. There is no external occipital protuberance. The infratemporal crests marking the outer limit of the superior head of the external pterygoid muscle are barely palpable.

3. The supraciliary bulgings are absent and the glabella ill-defined. The forehead is vertical and the supraorbital margins sharp.

4. The bizygomatic distance is remarkably short. The skull falls into the rare category of cryptozygy. No part of the zygoma is seen when the norma verticalis is viewed with the dioptograph; and, a further check, a ruler placed at right angles to the stand on which the skull was set, and brought up flat against the coronal suture, was still about 2 mm. outside the zygoma.

5. The third molar teeth are not erupted but in the lower jaw and the left maxilla are visible within the alveolar ridge. The left lower second milk molar is in position, the second premolar just showing at its side above the alveolar margin.

Discussion

(1) *Age*

The age of disappearance of the metopic suture varies greatly, but it usually occurs in the second year.

This would appear to be a case of persistent metopism. The cephalic index is 75, the skull reaching the lower limit of mesaticephaly, so there is no support here for

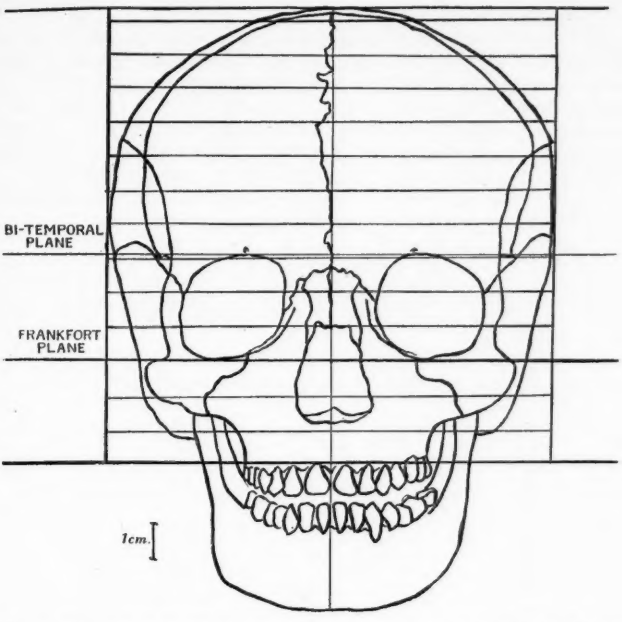

Fig. 1. Norma facialis. The horizontal lines between the lateral vertical lines are drawn parallel to the Frankfort plane 1 cm. apart.

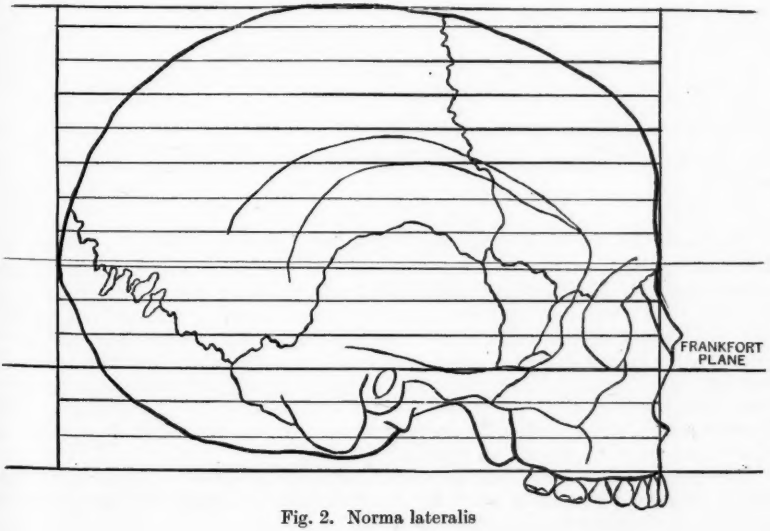

Fig. 2. Norma lateralis

associating metopism with brachycephaly. Bryce (1) found the average cephalic index of some 70 metopic skulls to be 76·07.

Synosteal closure of other vault sutures was found by Wingate Todd and Lyon, Jnr. (2) in their large series of male skulls not to begin until 22 years, except at the obelion, when ectocranial closure began at 20. They thought that sex had little influence on the time of closure.

Spheno-occipital union is said to occur between the ages of 18 and 25 (3). It is nearly complete in this 17-year old skull, only a vestige of the synchondrosis showing on both surfaces.

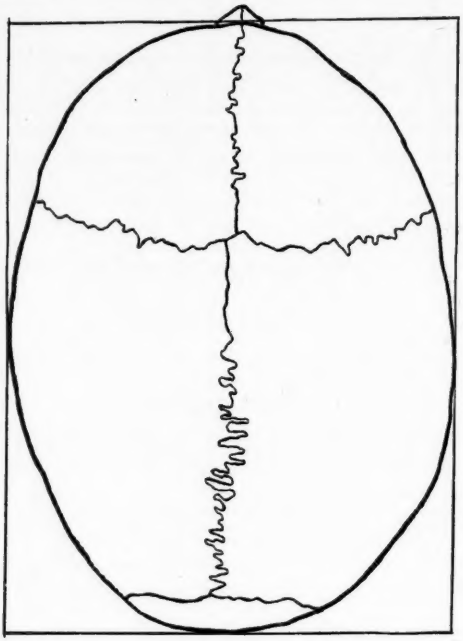

Fig. 3. Norma verticalis.

(2) *Sex*

The skull has the female characters of lightness, smoothness, vertical forehead, ill-defined glabella and sharp orbital margins. It has, further, the narrow bizygomatic measurement noted by Parsons and Lucas Keene (4). It does not conform in respect of two other measurements given by these authors as a test of sex, namely the cephalic and the auricular height/breadth indices. They found that, within the groups of heads and skulls measured, the female skull, in comparison with the male, suffered a greater loss of height and length than of breadth. This skull, on the contrary, has a remarkably low cephalic and a comparatively high auricular height/breadth index. But it is realised that these tests are applicable only to large numbers of skulls of the same racial and cultural grouping.

The palatal width, measured between tuberosities of maxillae (48 mm.), is below the average for females (54 mm.) found by Parsons and Lucas Keene (4), but the alveolar development is not complete.

Characters relating to mental development

The skull is that of an imbecile and the presence of stigmata was looked for.

In certain respects it certainly falls well within the category of "normal." It has a cranial capacity of over 1400 c.c.; the palate is not arched; and the pituitary fossa falls short by 1 mm. only in its antero-posterior and transverse measurements of Fitzgerald's average figures for adult male skulls.

So far this skull supports the view that, except in marked cases of microcephaly, mental development does not find any reflection in cranial form.

Measurements

Cranial capacity (by measurement with mustard seed), 1410 c.c.

	mm.
Height (basion–bregma)	127·5
Auricular height (auricular point–bregma)	114
Length (glabella–occipital point)	180
Breadth: Maximal	135
Bistephanic	120
Frontal (on temporal lines: minimal)	100
Base: cranial (basion–nasion)	93
Face.	
Height (pogonium–nasion)	101
Upper height (alveolar point–nasion)	62
Breadth (bizygomatic–maximal)	115
Base (basion–alveolar point)	86
Orbit.	
Right: Height (maximal)	31
Breadth (maximal)	37
Breadth (to dacryon)	35
Left: Height (maximal)	32
Breadth (maximal)	37
Breadth (to dacryon)	35
Nose.	
Height (nasion–root of nasal spine)	49
Height of aperture	30
Breadth of aperture (maximal)	23
Palate.	
Length	47
Breadth (between inner aspect of alveolar ridge at level of second molars)	35
Breadth (between centre of tuberosities of maxillae)	42
Lower jaw.	
Height: symphyseal	27
sigmoid	42
Breadth: biangular	84
bicondylar	10·3
Pituitary fossa.	
Height	8
Breadth	13*
Antero–posterior length	11

* Between middle clinoid processes.

Indices.		mm.
1. Cephalic:	$\frac{\text{Breadth}}{\text{Length}}$	75
2. Height:	$\frac{\text{Height}}{\text{Length}}$	70·6
3.	$\frac{\text{Auricular height}}{\text{Maximal breadth}}$	84·4
4. Facial:	$\frac{\text{Upper height}}{\text{Bizygomatic breadth}}$	53·9
5. Facial:	$\frac{\text{Total height}}{\text{Bizygomatic breadth}}$	87·8
6. Breadth:	$\frac{\text{Frontal}}{\text{Maximal}}$	74·07
7. Breadth:	$\frac{\text{Frontal}}{\text{Bizygomatic}}$	86·9
8. Breadth:	$\frac{\text{Bistephanic}}{\text{Bizygomatic}}$	104
9. Breadth:	$\frac{\text{Bizygomatic}}{\text{Maximal}}$	85·1
10. Alveolar:	$\frac{\text{Facial base}}{\text{Cranial base}}$	93·5
11. Nasal:	$\frac{\text{Breadth}}{\text{Total height}}$	46·9
Nasal:	$\frac{\text{Breadth}}{\text{Height of aperture}}$	26·7
12. Orbital: R.	$\frac{\text{Height}}{\text{Breadth}}$	83·6
L.	$\frac{\text{Height}}{\text{Breadth}}$	86·5

I have to thank Prof. Lucas Keene for the provision and preparation of the skull, and Prof. F. G. Parsons for much valuable advice and criticism.

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REVIEWS

Baillière's Synthetic Anatomy. By J. E. CHEESMAN. London: Baillière, Tindall & Cox. Parts I–XII, complete in binding case, 156 plates. Price 42*s.* nett.

The publication of this work has been completed by the issue of Part X—"The Brain." This part is arranged on the now familiar lines of its predecessors: in twelve transparent plates the gross anatomy of the brain and the arrangement of some of its main tracts are portrayed in successive oblique planes of section and dissection drawn rather larger than full size. The interpretation of these plates calls for more careful study than is required in dealing with some other sections of the Atlas, but such study will be repaid by the three-dimensional appreciation gained of the main topographical features of the brain and its blood vessels. The colour registering is here particularly good. The course of the great vein of Galen should be more correctly shown, in the light of Stopford's observations.

A study of the complete work confirms the appreciation already expressed in previous reviews of individual parts. It is a mine of topographical information which, if carefully worked, will give a rich yield. The student is forced to study solid structures, not merely flat pictures of the structures. This unique production calls for praise for the author, the publishers, and, it may be added, the author's one-time teacher of anatomy, now revealed in a Foreword as Prof. J. Ernest Frazer, the influence of whose teaching is likewise revealed in the work itself.

The neat binding case supplied is on the "loose-leaf" principle, and is capable of storing additional notes or diagrams made in the course of study.

Leitfaden der mikroskopisch-anatomischen Untersuchung pathologischer Objekte, des Blutes, und des Zentralnervensystems. Von G. C. VAN WALSEM, ehem. o. Prof. der pathol. Anatomie in Leiden, Haarlem (Holland). Mit 48 Abbildungen. Leipzig: S. Hirzel. 1932.

This little book of seventy-five pages represents a summary of those procedures which the author has found most serviceable and reliable in the course of his long experience in histological technique. Such observations had previously been scattered in some sixty-three publications by the author and have now been gathered together in this brochure. The book contains advice relating to the orientation and fitting of the laboratory. The author discusses the uses of a hand centrifuge, the regulation of gas flames, modifications of the Bunsen burner methods of decalcification and getting air out of the lung. He gives in detail his method of fixation, embedding and staining. The chapter on blood is especially interesting and contains the description of a method whereby in one preparation in the counting chamber it is possible to enumerate the red cells, the white cells, and the platelets, and at the same time to obtain a differential count. The name "panarithmetic method" is given to this.

Das Pollersche Verfahren zum Abformen an Lebenden und Toten sowie an Gegenständen. Von ALPHONS POLLER. (Berlin: Urban u. Schwarzenberg.) 1931. Pp. 1–216.

Dr Poller of Vienna has placed in our hands, in the form of the plastic material "Negocoll," a valuable adjunct to plastic art in medicine.

Negocoll is applied with a brush in a liquid state at body temperature. The mass

congeals to an elastic solid resembling rubber. This is removed in about ten minutes and yields a perfect cast. So accurate is the method that dermal ridges, openings of sweat glands, sulci of the brain, and minute details are correctly recorded. Since the mass is cooked before use it is aseptic and can be used even to obtain a cast of an open wound.

The numerous illustrations in the text depict clearly the various uses to which Negocoll can be put.

Die Veränderungen der Gewebe bei übermässiger Beanspruchung der Zähne. Von B. Gottlieb u. B. Orban. (Leipzig: Georg Thieme.) 1931. Pp. 7–225. Price M. 27.

This monograph by Gottlieb and Orban of Vienna is a detailed description of a series of experiments on thirty-three dogs and five apes with a view to determining the alterations in the tissue of the jaw due to increased or decreased work thrown upon the teeth. Certain teeth were filled or capped in such a way that the resulting asymmetry of the bite led to an alteration of the thrust and strain on the bony framework of the jaw. The right and left teeth were sectioned histologically *in situ* and the resulting changes in the architecture of the jaw are clearly displayed. The rate of absorption and deposition of new bone in proximity to the roots of the teeth subjected to unusual stresses is indicated.

Increased work thrown on a tooth leads to elongation of the roots and the primary absorption of alveolar bone is followed by the secondary deposition of more bone. The practical application of these experimental results to Man is of great importance and the various methods of controlling the bite and occlusion of the teeth are discussed.

One of the most interesting experiments traces the changes in the tooth and jaw after pulp extraction. The root, cement and bone become strictly continuous with one another after a period of primary absorption, whereas in the cases of a root left in the jaw after extraction, the bone never becomes continuous with the cement. By extracting one tooth so as to reduce and almost eliminate the function of its antagonist it is proved that the periodontal space of the latter is reduced.

The illustrations and microphotographs of this monograph are of a very high order.

Leitfaden für Situsübungen an der Leiche. Von Dr Med. W. Pfitzner. (Leipzig: Franz Deuticke.) 1931. S. 37. Price M. 1.40.

A little pamphlet on the routine examination of the great body-cavities in the normal subject, written by Dr Pfitzner, late Professor of Topographical Anatomy in Strassburg, deserves notice. Short and unpretentious as it is, it contains an idea which should be of some interest to students, and is probably the outcome of Professor Pfitzner's experience as a teacher. The systematic examination in detail of the body-cavities, as conducted in post-mortem examinations, is a considerable undertaking. When a student comes to this work it is a common experience that his performance is anything but satisfactory, the reason being, not necessarily lack of knowledge, but that during his anatomical studies he has had no practice in the routine, as indeed in the nature of the case it is impossible he should have. Professor Pfitzner has endeavoured to supply something by way of a substitute for routine practice. The first section of his pamphlet merely gives a list of structures to be examined *in situ* in the several cavities, in the order in which they are met with. The second section goes over the same ground, but with the addition of the details

of form and relationship which are mentioned in the course of an actual demonstration, and which would be verified to the student. The pamphlet, therefore, gives the student a means of recapitulating mentally every step of the demonstration that he has witnessed. The booklet has found favour with students for the better part of half a century, and if used fairly, not as a cram-book but to recall from time to time the steps of an actual demonstration, the student would probably realise the value of it in the later stages of his career.

Die Histogenese ekto-mesodermaler Mischgeschwülste der Mundhöhle. Von P. Schürmann, H. Pflüger u. W. Norrenbrock. (Leipzig: Georg Thieme.) 1931. Pp. 1–94. Price M. 11.50.

This monograph deals with mixed tumours of the oral cavity and puts forward a theory of ectomesodermal tumours, of which the parotic tumour is a type, in terms of epithelial rudiments which act as "organisators" in Spemann's sense of the term.

It is held that the development and differentiation of the mesodermal elements of the tumour are controlled and determined by the epithelial components. This point of view enunciated by Dr Pflüger of Hamburg and Dr Schürmann of Berlin has also been applied by them to tumours of the hypophysial duct and of the dental-forming tissue.

A special consideration of the histology of mixed tumours of the parotid gland by Dr Norrenbrock of Hamburg analyses the ectodermal and mesodermal components with the aid of numerous photomicrographs.

Anatomie des Lymphatiques. Par H. Rouvière. (Paris: Masson.) 1932. Pp. 1–489, 129 figs. Price 150 francs.

This book is a monograph on the anatomy of the lymphatic vessels and the glands as they are disclosed by the method of injection. The description is arranged in systems, describing first those of the head and neck, then the thorax, and then the extremities and finally the abdomen and pelvis, and the terminal vessels. In each of these regions of the body the lymphatic circulation is described, as it forms a collecting system for the principal organs.

There is a short introductory chapter containing a few general remarks on lymphatics, but there is no exhaustive description of the nature and meaning, evolution, development, and the place of the lymphatic circulation in the economy of the body. No adequate discussion is given of the absence of lymphatics from some parts of the body. For instance, the question of the relation of lymphatics to the nervous system is dismissed in a few lines with some remarks about the distribution of tetanus toxins. Despite a great many observations to the contrary and the opposition of clinical facts the author seems to accept the possibility that lymphatics may communicate with veins in many places, the liver for instance.

The description of the disposition of the glands draining the head and neck is more detailed than that given in Poirier and Charpy and includes some glands which the author has discovered deep to the splenius. The tongue follows closely and confirms the description given by Poirier. There are three places where spread of lymph may occur to the opposite side: (1) The submucus lymphatics; those of the anterior part he maintains are distinct from those draining away from the posterior part of the tongue. (2) In the posterior lymphatics where they digress to either side of the midline. (3) The median lymphatics which descend between the genio-glossi and genio-hyoids.

The lymphatics of the thyroid are described in a way which follows earlier descriptions and the author records he has found no evidence of the arrangements suggested by Scott Williamson.

The description of the lymphatics and the lymph nodes of the lung is far more detailed than that supplied in Poirier and Charpy's account. The nodes are classified as they occur about the trachea, then around the primary bronchi, and then in the root of the lung and finally as intrapulmonic. The author is sceptical of the existence of lymph nodes far in the substance of the lung. At any rate the methods he used did not disclose the existence of these nodes. The drainage from the lobes of the lungs is not entirely independent, but anastomoses occur between adjacent lobes and in the root of the lung the nodes subserve always more than one lobe of the lung.

The book gives an extremely detailed account of the lymphatics and the nodes for all the organs of the body and will surely be the source from which the surgeons will borrow their illustrations of lymphatics in future as they have done in the past from Poirier and Charpy. It is more detailed than Poirier and Charpy. The author has taken pains to make it accurate, for not only is it based on his own enormous researches but he has been assisted in his work by many colleagues. It is abundantly illustrated and there is a full bibliography.

Anatomy of the Human Orbit and Accessory Organs of Vision. By S. Ernest Whitnall. Second Edition. (Humphrey Milford. London: Oxford Univ. Press.) 1932. Pp. xii + 469, 212 figs. Price 25*s.* nett.

That a second edition of this monograph should have been called for at the present time is alone an indication of the important position that it already holds. Since anatomists and ophthalmologists alike concur in considering it at once a standard work of reference and an invaluable text-book, there is but little need to labour its praises.

Designed originally as a commentary and résumé of the course of Anatomy for the Oxford Diploma of Ophthalmology it became in preparation easily the most exhaustive treatise available on the subject. The second edition preserves the good points of the first, the clarity of its language, the wealth of pictorial and descriptive detail and the valuable and exhaustive references with which it abounds. A large number of important papers bearing on the subject have appeared since 1921 and their salient features have been incorporated in the book. In addition at least a dozen new diagrams and photographs are included and many of the older ones improved by the use of colour. The major part of the additions is to be found in the sections dealing with the nerves and their cerebral connections. Thus Wolff's clinically important diagram of the bend in the VIth nerve and Stibbe's microdissection of the communications of the Vth are now included, as also the work of Nicholson on the orbital ganglia and Schaeffer on the chiasmal region. Finally, the section dealing with the cranial nerve nuclei has been amplified and brought up to date.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

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PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

NOVEMBER, 1931

THE Annual Meeting of the Society was held at the London Hospital Medical College on 27 November, 1931.

Professor WILLIAM WRIGHT, the newly elected President, took the chair and gave an inaugural address on anatomy as it was known at the time of Andreas Vesalius.

Dr F. GOLDBY read a paper on the "Paraterminal body of Reptiles," of which the following is an abstract.

The paraterminal body was defined for the brain of *Lacerta viridis*, as that area of the medial hemisphere wall situated between the clear-cut ventral edge of the hippocampal cortex dorsally, the tuberculum olfactorium ventrally and superficially, and the palaeostriatum ventrally and deeply. Anteriorly it extends into the root of the olfactory peduncle where it merges with an undifferentiated cortical layer of cells which surrounds the ventricle in the peduncle. Posteriorly it extends to the lamina terminalis and the anterior and hippocampal commissures, and also above the hippocampal commissure and foramen of Monro, to a region in the medial hemisphere wall just behind the commissura aberrans or the posterior pallial commissure of American and continental authors. This was the definition given by Elliot Smith when he first applied the name "Paraterminal Body" to this region in 1901. The paraterminal body is well developed in *Lacerta viridis*, and clearly defined. It was illustrated by drawings of transverse sections and by a sketch of the medial surface of the cerebral hemisphere on which the extent of the paraterminal body and the position of the nuclear differentiations within it were plotted. The most conspicuous differentiation occurred in the part of the paraterminal body between the lamina terminalis and the olfactory peduncle, where a dorso-lateral large-celled and a ventro-medial small-celled nucleus could be seen. This is the region which receives the greater part of the fibres of the median fore-brain bundle. Anteriorly, near the base of the peduncle, the paraterminal body contains few cells, except ventrally where a fairly compact small-celled nucleus could be seen; possibly a nucleus of the medial olfactory tract. Posteriorly clearly defined nuclei of the diagonal band of Broca and of the hippocampal and aberrant commissures could be seen. There was no definite nucleus of the anterior commissure and the few cells accompanying its fibres appeared to belong rather to the striatal complex than to the paraterminal body. It was suggested that the terms nucleus accumbens septi and primordium hippocampi should be dropped, since the former does not belong to the paraterminal body at all but to the striatal complex, and the latter is both misleading and unnecessary when it is applied to any part of the paraterminal body. This description of the paraterminal body for *Lacerta viridis* agrees very closely with the description given by Durward (*J. Anat.* 1930) for

Sphenodon, and, when allowance has been made for differences in terminology, is at least not inconsistent with published descriptions of other Lacertilia, and of Crocodilia and Chelonia. It appears to be the fundamental plan on which the reptilian paraterminal body is built. The paraterminal body consists essentially of nuclei developed in connection with the commissures, and in connection with fibre tracts which are afferent to or efferent from the hippocampus.

In the discussion which followed Dr Goldby's paper Dr A. DURWARD remarked that the Reptile *Sphenodon* has a well-defined paraterminal body with two large and distinct septal nuclei, a lateral large-celled and a medial (and ventral) small-celled nucleus. The condition described by Dr Goldby was essentially the same as that in *Sphenodon*.

Professor LE GROS CLARK congratulated Dr Goldby on his clear exposition of a very difficult subject. He was impressed with the remarkable similarity in the structure of the paraterminal region in *Lacerta* and primitive Insectivores such as *Macroscelides*. He entirely agreed with Dr Goldby on the points which he raised regarding the nomenclature of this region.

Professor LE GROS CLARK showed sections of the lateral geniculate bodies in two cases (monkey and human material) in which one eye had been destroyed some time before death. In both cases the unilateral optic atrophy had been followed by chromatolytic changes sharply circumscribed in alternate cell laminae on both sides. If these laminae are designated from the superficial aspect as laminae 1*a*, 1*b*, 2*a*, 2*b*, 3*a* and 3*b*, then it appears certain that crossed fibres of the optic tract terminate in laminae 1*a*, 2*b* and 3*b*, while uncrossed fibres end in laminae 1*b*, 2*a* and 3*a*.

The following took part in the discussion on Professor Le Gros Clark's communication:

Dr ZUCKERMANN said that in the phylogeny of the Primates, a separation had occurred between lemurs and ordinary monkeys. The lamination of the geniculate bodies appears to be a correlation of structure with function. He alluded to the experiments of Pawlov on dogs, and said that dogs were found to be unable to distinguish parallel from vertical lines, although they were able to distinguish an oval from a circular disc. The power to distinguish form was correlated with binocular and stereoscopic vision.

The PRESIDENT enquired whether the number of fibres going into the lateral geniculate body was equal to the number of those going out.

Professor LE GROS CLARK in reply said that it was extremely difficult to estimate the number of fibres passing to or from the geniculate bodies. Fibres from the tract passed directly to the pretectal nuclei.

Professor BRASH exhibited some specimens showing symmetrical thinning of the parietal bones. They were bones of Cingalese women. The thinning of the bone affects the outer table only, the erosion passing right through the outer table into the diploe. The second specimen shows the same condition on one side, with heaping up of the bone of the outer table. The condition was a senile change. It was stated that certain native races wear a horseshoe-shaped comb which may cause pressure on the skull.

Sir ARTHUR KEITH said that the thickening of the bone ceases before reaching the temporal ridges. In his opinion the condition was one not due to pressure but to nutritional changes.

Dr E. P. Stibbe gave a demonstration on "A rare case of diaphragmatic hernia."

Professor Fawcett asked whether muscle fibres were found in the wall of the sac, to which Dr Stibbe replied in the negative.

Professor West enquired what was the cause of the rotation of the stomach, and mentioned a case of an adult with duodenal hernia in which the radiologist described the bismuth meal as going in at the bottom of the bend and coming out at the top.

Dr Harris mentioned a case which was first diagnosed as a left pleural effusion with displacement of the heart to the right. It was afterwards thought to be a case of pneumothorax. One physician had seen the patient when the stomach was distended with fluid, the other when it was full of gas. Diaphragmatic hernia is relatively infrequent in domestic animals as compared with Man.

Dr Durward stated that he had seen a case of diaphragmatic hernia in a stillborn child (presenting iniencephaly) in which the defect was in the left antero-lateral muscular part of the diaphragm. The spleen, carrying with it the gastrosplenic and lienorenal ligaments, was the only abdominal viscus within the thorax. There was no evidence that recent trauma had produced the condition.

The President said that this greater frequency in Man might be accounted for by the relatively greater width of the thorax in Man as compared with that of quadrupeds.

Dr Stibbe in reply said that the displacement of the duodenum mentioned by Professor West might be explained by considering that the extreme end of the duodenum had been caught at the time of rotation and nipped in the hernial sac.

Professor Fawcett demonstrated "Reconstruction models of the crania of two South American monkeys, *Mycetes seniculus* and *Cacajas Melanocephala*."

Professor Le Gros Clark asked for information regarding the development of the premaxillary element in the Primates, with special reference to the suggestion made by some authorities that there is a fundamental difference in its developmental history in Man as contrasted with the anthropoid apes and the Pithecoidea.

Professor Fawcett replied that in Man the premaxilla unites very early with the maxilla on the surface or superficial aspect. In lower Primates it remains separate. The palatine segment of the premaxilla appears to develop as a separate centre.

Professor Fawcett also exhibited the skull which had been discovered in the Cave of Lombrives.

Dr A. Durward read a paper on "The brain of the Kiwi," which will be submitted for publication in the *Journal of Anatomy*.

Dr Claire Weekes read a paper on "Factors determining viviparity in Reptiles."

She referred to the influence of factors such as endocrine activity, climate and more especially variations in temperature and degree of humidity, in determining whether one group or another would be viviparous or oviparous. Certain tropical sea snakes have both viviparous and oviparous species.

The PRESIDENT asked whether competition was a factor which would influence the condition, and mentioned the dodo now extinct owing to the introduction of pigs into the country which ate the eggs.

Dr ZUCKERKANDL said that he was not quite persuaded that climatic factors were the sole factors determining the condition. The theory implied a peculiar linkage of heredity and environment. He instanced the adder and the grass snake. One has developed its viviparity on the spot. The other became viviparous. He asked why the animal does not change its habit, and suggested that the conditions might be brought about by mutations.

Dr WEEKES in reply said that there was no evidence of the conditions of viviparity or oviparity being determined by mutations and that it would take many thousands of years for any species of animal to change its habits. The polar bear brought to a warm climate will not change its habits because it will not rear cubs, which if they lived might carry on any changes that might result from change of climate.

FEBRUARY, 1932

An ordinary meeting of the Society was held in the London School of Medicine for Women on 5 February, 1932, the President, Professor WRIGHT, being in the Chair.

Dr G. MURRAY LEVICK read a paper on "The rôle of the vastus internus."

Hitherto the action of vastus internus muscle has only been described with the other muscles which together form the quadriceps extensor cruris.

It would appear, however, that with the exception of the circumstances when it is required to assist in a very powerful extension movement, the vastus internus may act independently. Its action is easily demonstrated as follows: If the sitting position is assumed, and a couple of fingers of one hand kept on the belly of the muscle just above and internal to the knee-joint in order to palpate it, when the knee-joint is gradually extended it will be observed that whereas the rectus femoris, vastus externus and crureus are contracting forcibly from the moment the movement commences and throughout the extension, the vastus internus is virtually quiescent until the final full extension of the joint is attained, when it contracts forcibly and remains contracted.

It is seen, in fact, that the rôle of this muscle is the locking of the knee in full extension, its steadying effect being enhanced by its insertion along the inner border of the patella. This action, coupled with the fact that it does not take part with the rest of the quadriceps muscles throughout the extension of the joint, explains why its hypertrophy is so noticeable in rowing men, who are taught to lock the knees hard back in order to impart the final "drive" at the finish of the stroke.

In walking, it is primarily responsible for maintaining the full extension of the knee-joint of the supporting lower limb while the body and the leg which is off the ground are being carried forward. This has an interesting bearing upon a common experience in orthopaedic practice, viz. that inflammation of the knee-joint is accompanied by loss of tone in the quadriceps muscles due to the reflex effect of the inflammation through the anterior crural nerve which enters largely into the innervation of the knee-joint especially through its branch to the vastus internus, which supplies the synovial membrane. When

a pressure bandage has been applied to the joint in order to reduce the synovial effusion, this loss of tone is, in the case of the vastus internus muscle, accompanied by wasting from the pressure of the bandage.

When such a patient is at length allowed to go out and walk, frequently the affected joint gives way, without any warning, at the moment when it should support the entire weight of the body because the opposite foot is off the ground, and the patient falls, straining the internal lateral ligament. This accident may take place time after time in the same patient. In orthopaedic practice this well-known symptom is ascribed to loss of tone in the quadriceps generally, but I believe it is the failure of the vastus internus in particular which causes the accident, because this muscle is primarily responsible for locking the knee in full extension.

Using a living model, Dr MURRAY LEVICK demonstrated the action of the vastus internus as explained in his paper.

Dr G. MURRAY LEVICK also read a paper "On the arch-raising rôle of certain intrinsic muscles of the foot."

In the course of some experimental work shortly after the War, I happened to discover that certain intrinsic muscles of the foot had an important rôle which I have not seen mentioned in any anatomical or other work. I published this observation in one of the medical journals, but it appeared to escape general notice and I therefore welcome this opportunity afforded by your kind invitation to bring my observations before you to-day for discussion.

First, I will consider the dorsal interosseous muscles of the foot.

If the foot, or at any rate the toes, are off the ground to such extent that the metatarsal bones are the fixed points from which the dorsal interossei act, the action of these muscles is to move the toes in the way that has hitherto been laid down in describing their action, and which I need not repeat.

If, however, the foot is on the ground, with the weight forward on the toes which are pressed against the ground, the first phalanges into which the tendons of the muscles are inserted become fixed points instead of movable points, and owing to the bipênniform origin of each muscle from adjacent metatarsal bones, its contraction results in drawing these two bones towards one another. The simultaneous action of all four dorsal interossei, with the toes fixed, is to bunch up all the metatarsal bones in such a way as to raise the transverse arch, the second metatarsal bone being the keystone of the arch since the first phalanx of the second toe has the tendons of the first and second dorsal interossei attached to it, one on each side. The second metatarsal bone consequently remains stationary while the other metatarsal bones are adducted towards them.

This effect of raising the transverse arch is a powerful one and takes place most strongly when it is most needed; for instance, when the individual is running, walking or jumping on the toes, and at the moment in walking when the weight of the body is carried forward on to the front of the rear foot as it propels the body onwards.

The pathological flattening of the transverse arch of the metatarsus, which is often the cause of serious disability, is, I think, generally due to atrophy of the dorsal interosseous muscles and this atrophy would naturally follow the wearing of narrow boots or shoes which act as leather splints compressing and thus putting these muscles out of action.

In emphasising the above factors I do not exclude the already recognised

arch-raising action of adductors transversus and obliquus hallucis, but I suggest that the action of these muscles is of rather secondary importance.

My next observation is the powerful longitudinal arch-raising action of flexor brevis digitorum and flexor brevis hallucis.

When the weight of the body rests on the anterior arch of the foot, with the heel off the ground, these muscles, instead of flexing the toes, draw the os calcis towards them with a powerful bowstring action, raising both longitudinal arches.

They are, in fact, very powerful arch-raisers and support these arches at the critical moment of springing on or off the toes. By electrical stimulation I hope to prove to your satisfaction the correctness of the views I have advanced. They seem to me of importance chiefly in throwing fresh light upon the causation and treatment of various forms of pesplanus. By a method of Faradic stimulation, Dr MURRAY LEVICK then demonstrated on a living model the raising of the longitudinal and transverse arches of the foot by the short toe flexors and dorsal interossei respectively.

The PRESIDENT, in discussing Dr Murray Levick's papers, said that the dorsal interosseous muscles of the foot may act from their insertion to their origin, and he considered they had very little abducting or adducting action. A good illustration of a muscle acting from its insertion to its origin is that of the serratus magnus which may act as a muscle of inspiration when the scapula is fixed. He also commented on the locking of the knee-joint in extension, saying that the movement producing the fixation was rather an internal rotation of the femur on the tibia than an outward rotation of the tibia on the femur. Cats had the power of spreading their claws and drawing them in, but he doubted whether the dorsal interossei of the human foot had any power of abducting or adducting.

Dr TUDOR JONES read a paper on "The conducting mechanism in the heart of *Lepidosiren paradoxa*," of which the following is a summary.

He demonstrated sections of two larval stages, 36½ and 37 (Keibel), stained by Bielschowsky's method; wax plate reconstructions of the heart in these larvae and of the cranial roots of the vagus and related nerves; and Bielschowsky-stained sections of a human embryo 24 mm. long and of the medulla oblongata of a salmon larva of 10 mm.

The material demonstrated the cardiac nerves of *Lepidosiren* in the following parts of their course, viz. their dorsal ganglia and ventral roots, with the nucleus of termination of the dorsal component and the situation of the nucleus of origin of the ventral root on one side; the left nerve in relation to the ductus Botalli, uniting the Vth and VIth arches, and to the pulmonary artery; and the nerve of each side converging to join its fellow in the dorsal mesocardium before taking part in the formation of a complex intracardial system. This system was shown in section at three levels: (1) within the pulmonary ridge, investing the termination of the pulmonary vein, (2) bifurcating in the roof of the atria to form a band encircling the atrio-ventricular opening, and (3) parts of this nervous ring. The whole formation was indicated on the wax reconstructions of serial sections and separately demonstrated by wire models representing the nervous parts only. These showed the formation of a closed series of loops (1) surrounding the sinu-atrial opening, (2) surrounding a large area of the dorsum of the sinus, and (3) surrounding the atrio-ventricular opening. In all these situations the nervous formation was

shown in the sections in close relation with the endocardium. The union of the loops was effected by junctions (1) in the roof of the atria, (2) on the intracardial surface of the ventricular plug (septum), and, to each side of the septum, by bands in the sino-atrial boundaries. From the union of the rings on the ventricular septal surface, extensions were shown passing to the ventricles. The situation of this nervous formation was compared with the described situation of the conducting mechanisms, both nervous and "specialised," in other animals; and it was stated that the nervous formation in *Lepidosiren* occupied all the situations in which the conducting mechanisms of other animals had been found, although striation of the muscle was only commencing and no muscular elements were visible in the walls of the sinus venosus and atria. The section of the human embryo illustrated the foam-like appearance of the nerves (the phrenic and cardiac were shown for convenience) in their early stages before nuclei appeared along their course, and while still reticular. At one of the stages of the *Lepidosiren* shown, the greater part of the system of nervous rings described was represented by a similar reticular formation condensing in places into formed nervous elements, the whole being in continuity with the cardiac nerves described and in relation, apparently at three points, with minute nerve bundles from another source. The material, and similar material of earlier stages, provides evidence bearing upon the mode of development of the conducting system and upon its morphology. Since the cardiac nerve in *Lepidosiren paradoxa* is distinguishable from other visceral components by a peculiarity of its fibres; and since it incorporates, apparently in a single neuro-visceral complex, the lower arches, the pulmonary arteries, the lungs and the cardiac tube throughout its extent, it provides evidence bearing upon the morphology of these parts. Later Dr Tudor Jones hopes to submit a discussion of some of these points in a form suitable for publication in the *Journal of Anatomy*.

Dr GLADSTONE congratulated Dr Tudor Jones on his extremely interesting and important work and remarked on the essential similarity of the conducting system in all classes of Vertebrate animals which has been demonstrated by various workers on the subject, and more especially recent papers of Dr F. Davies on the conducting mechanism in Birds, in which class of Vertebrates its existence had formerly been denied. He also remarked on the apparent continuity of tissue, which was evidenced by the specimens demonstrated, in the development of the neural and muscular components of the system.

Professor BLAIR asked whether Dr Jones had been able to demonstrate a direct connection between the sinu-auricular node and the atrio-ventricular canal.

Professor WRIGHT said that it was remarkable to find that all the important elements in the mammalian heart are present in so low a type as the Dipnoan, and that there was a continuity of plan in all types of animals both high and low, whether there is a pulmonary or branchial type of circulation.

In reply to Professor Blair, Dr JONES said that there is abundant evidence of a connection between sino-auricular node and the tissue of the atrio-ventricular canal; there is also a continuity of the nerve tissue in the heart with the reticular or marginal layer of the neural tube.

Dr M. A. MACCONAILL read a paper on "The ultimate forms of diarthrodial joint surfaces," which will be submitted for publication in the *Journal of Anatomy*, and of which the following is a short summary.

The surfaces of diarthroses are of such shapes that a thin film of synovial fluid, of definite form, can be formed between them during movement, ceasing to exist when motion stops. They also have a large area of complete congruence in one position, the synarthrodial ("weight-bearing") phase. From these premises can be deduced the ultimate forms and movements of the surfaces, and the deductions are found to be in complete agreement with observation. The paper was preceded by an electrical demonstration of the complete separation of the surfaces of a synovial joint (elbow) during movement, oil of suitable viscosity being used instead of synovia.

Dr YOFFEY read a paper on "Intestinal lymphoid tissue in Mammals," which will be submitted for publication in the *Journal of Anatomy*.

Professor T. B. JOHNSTON, Dr ODGERS, Professor WRIGHT, Dr MACCONAILL, and Dr TUDOR JONES took part in a discussion in which the origin, distribution, function and age changes of lymphoid tissue were dealt with.

In reply to the question raised by Professor Johnston regarding the protective function of lymphoid tissue Dr YOFFEY said that in old age when the lymphoid tissue has disappeared the parts to be protected are less liable to be inflamed than in the young. Dr Yoffey did not regard the reticuloendothelial system as a distinct system apart from other tissues.

The PRESIDENT remarked incidentally that reticuloendothelium was not discovered by Aschoff but by Dr Shore.

Dr LILIAN M. DICKSON described "A rare arrangement of the deep extensor muscles of the fingers and thumb."

The specimen, a right forearm and hand, was obtained from the dissecting room.

The deep extensor group of muscles was unusually well developed. In addition to an abductor pollicis longus and an extensor pollicis brevis there were found taking origin from the ulna in the order here stated and from above downwards (1) an extensor pollicis longus, (2) a muscle whose tendon divided, one half passing to the thumb, the other to the index finger (this muscle may conveniently be called an extensor intermedius), (3) an extensor indicis proprius, and (4) an extensor medianus proprius.

The insertion of the extensor pollicis longus was unusual. The greater part of its tendon was inserted into the radius at the proximal end of the groove in which the tendon normally lies. A slender slip passed downwards to the thumb.

On the back of the thumb a flat tendon was present, inserted into the base of the second phalanx. It was made up of the following parts:

(1) the slender slip from the extensor pollicis longus,
(2) the slip from the "extensor intermedius,"
(3) a slip from the base of the radial tubercle,
(4) a fan-shaped sheet from the posterior annular ligament.

A muscle similar to the "extensor intermedius" is normally present in certain Carnivores and other Mammals. Rare in Man, it usually replaces the long extensor of the thumb or the proper extensor of the index finger. In this case it co-exists with these muscles, but functionally it replaces the extensor pollicis longus.

The reason for the interruption of the extensor pollicis longus is not manifest. The additional origin of the distal part of the tendon from the

posterior annular ligament is probably a functional adaptation to correct the ulnar deviation consequent on extension of the thumb by the "extensor intermedius." The origin recalls some cases of the rarely present extensor manus brevis.

Dr Lilian Dickson also read a paper on "The relations of the Clivus," which will be submitted for publication in the *Journal of Anatomy*.

Professor Lucas Keene and Miss E. Hewer exhibited a series of specimens illustrating myelination of nerves in the human foetus and infant.

Dr M. A. MacConaill gave an electrical demonstration of the formation of pressure films in the elbow-joint.

APRIL, 1932

An ordinary meeting of the Society was held at St Mary's Hospital Medical School on 28 April, 1932, the President, Professor William Wright, being in the Chair.

Professor Frazer gave a short account of a very young human ovum *in situ*. It was obtained post-mortem from a patient of 35 who died from acute pancreatitis after an abdominal operation. Marked toxaemia for some time before death probably accounted for the ovum not being in as good condition as the decidua. The ovum lay in the superficial part of the compact stratum, in which there was definite decidual change. It measured, from trophoblast to trophoblast, $2 \times 2{\cdot}1 \times 1$ mm. The two minute embryonic vesicles lay against the basal chorion: the amniotic vesicle $0{\cdot}15 \times 0{\cdot}14$ mm., and the yolk sac vesicle $0{\cdot}1 \times 0{\cdot}13$ mm. The cavity within the ovum was lined by a thin coagulum next the chorion, in which were a few layers of mesodermal nuclei, falling to a single layer on the capsular side. The villi were in general small and stumpy, though several had progressed far enough to show some division. They were largely connected with the transitional region by trophoblast, plasmodial and cellular. The intervillous space contained a considerable amount of blood. Many large blood sinuses had been freely opened up, and a large number of glands cut through by the trophoblastic extension. The capsular decidua, which had made a slight convexity on the surface of a fold at the top of the posterior wall of the uterus, was thin. No definite or certain remnant of an aperture of entry had been found up to the moment. The woman's stay in hospital had been 10 days. She was married, and had had children. No history of any sort could be obtained, but the ovum, which would appear to be—or to have been, at the time of its death—of about the same degree of development as that of Jung's, is assumed to have been about 15 days old.

A full account of the specimen submitted for publication will be published later in the *Journal of Anatomy*.

In the discussion which followed Professor Grosser said that in his opinion the embryo had failed to grow for from 2 to 4 days before the death of the mother, and that this might account for the relatively large size of the amniotic vesicle. The growth of the embryo was probably affected by a toxic condition.

Professor Florian said that he possessed two embryos of about the same

age. There was a great difference in the size of the yolk sacs. Both embryos were very well fixed. In one which was obtained 12 hours after the death of the mother, there were very large blood spaces around the chorionic vesicle.

Professor HILL enquired into the relation of the primary mesoderm to the proliferated ectoderm, and said that the relative size of the amniotic vesicle as compared with the entodermic vesicle appeared to be correlated with a retardation of growth which prevented the growth of the embryo as compared with the growth in size of the chorionic vesicle.

Professor FRAZER in reply said that a relatively large amnion was a sign of an early stage in development. There were also certain cases in which the large size of amnion was the result of pathological changes.

Dr JOHN KIRK read a paper on "A case of "Megacolon," which will be submitted for publication in the *Journal of Anatomy*.

Professor BARCLAY-SMITH alluded to a similar case which he had described in the *Journal of Anatomy* and enquired whether Dr Kirk had examined the contents of the bowel and what was the mental condition of the patient.

Reply: The contents of the bowel were semi-solid. Dr Kirk could not make any definite statement with regard to the mental state of the patient except that the subject came from a "Poor Law Institution."

Professor WOOLLARD referred to the neuro-muscular condition as functioning normally behind a thin constriction. The neuro-muscular system he suggested might have been affected secondarily. It was he said very remarkable that Meissner's plexus was not involved.

Sir ARTHUR KEITH said that in his opinion these cases presented an anatomical rather than a pathological problem. Auerbach's plexus was hypertrophied in the first case examined by the speaker. In a second case, obtained from a man who was a subject of acromegaly, there was a generalised hypertrophy of the muscular and fibrous systems of the whole body. The condition may start at any time of life. Auerbach's plexus seemed to be primarily secretory in its mode of action, setting free a substance which stimulates the musculature of the bowel. In other cases of megacolon the muscle fibres seemed to be overladen with glycogen. In these cases there is a lack of co-ordination of the muscular contractions. The condition is like fibrillation of the heart, and comparable to the hypertrophy of the heart which results from stenosis.

Professor WRIGHT said that he was inclined to think that the primary cause was to be found in a defect in Auerbach's plexus rather than stenosis. In the elephant he had found an enormous hypertrophy of the tunica muscularis mucosae. Many of these conditions probably commence as a congenital defect, and the primary defect afterwards becomes aggravated by other factors.

Dr KIRK in reply said that cell nests were disseminated in parts of the plexus. The pelvic colon was so much distended that it touched the gall bladder and was stained with bile. The part of the colon which had become distended was the part provided with a mesentery. There was no stricture in the rectum, although the right valve of Houston was large and formed a shelf-like projection.

Dr YOFFEY gave a brief account of some investigations into the problem of lymphocyte production. By inserting a cannula into the thoracic duct of a

dog it was possible to collect the major part of the lymph. The flow of lymph was found to be remarkably even—in a 10 kg. dog about 25 c.c. per hour.

The cell content of the lymph thus obtained was estimated by performing hourly lymphocyte counts. In this way it was possible over a given experimental period to ascertain the number of fresh lymphocytes which would have entered the blood. At the same time the total lymphocytes in the blood stream were known from the blood volume and the lymphocyte count per cubic millimetre.

On comparing these sets of figures, the astonishing fact emerges that the lymphocytes of the blood, in young animals, are replaced about three times daily.

There appears to be a definite age factor involved. In older animals the lymphocyte production falls considerably. Whereas in dogs one or two years old the thoracic duct lymph has 10,000–16,000 lymphocytes per cu. mm. In a seven year old dog the count is usually only 3000–4000.

Finally, Dr YOFFEY gave the results of some chemical analyses to show that the fat content of lymph, in spite of its milky white appearance, was much less than was generally thought to be the case, and that the rôle of lymph in fat absorption must be very slight.

Miss IDA C. MANN gave a demonstration of the macula of *Sphenodon*. The opportunity having arisen for the examination of a live *Sphenodon*, drawings were made of the iris and the fundus. The latter showed an arrangement of nerve fibres and macula, similar to that seen in Man. Specimens of embryonic stages of *Sphenodon* from Professor Dendy's collection were examined, and two early stages of the macula described. In these the macula was represented by an increase in thickness of the retina above and to the temporal side of the disc. The stage of differentiation was similar to that of a 110 mm. human foetus. This is in confirmation of the work of Kallins, 1899, and Baze, 1912.

Professor WRIGHT spoke of colour vision in animals and raised the question as to whether colour vision is dependent on the presence of a macula and also the extent of distribution of a macula among Mammals.

Professor BARCLAY-SMITH remarked that colour vision was well developed in many invertebrates, e.g. mosquitoes and flies.

In Mammals a well-developed macula was found only in Primates. A dog can distinguish between variations in the relative intensity of illumination of different colours.

Professor LE GROS CLARK read a paper on the lamination of the lateral geniculate body in the Primates. Evidence was adduced to show that the six-layered type of nucleus characteristic of most Primates is derived from a trilaminar type. The folding of the laminae has occurred in different directions in the Lemuroidea and the Anthropoidea. In the former, the laminae have become folded inwards, producing an inverted type of lateral geniculate body, while in the latter an everted type has been formed. It was concluded, on these grounds, that the Lemuroidea and the Anthropoidea must have diverged at a stage when the lateral geniculate body was of a simple type, the laminae showing neither inversion nor eversion.

Professor BARCLAY-SMITH on behalf of Mr R. W. HAINES read a paper on "The investing layers of the body," which will be submitted for publication in the *Journal of Anatomy*.

JUNE, 1932

The Summer Meeting of the Society was held in the new Hambleden Department of Anatomy in King's College, London, on 24 and 25 June, 1932. The President, Professor WILLIAM WRIGHT, being in the Chair.

Dr TUDOR JONES read a paper on "The cardiac conducting mechanism in a human embryo (24 mm.)." He demonstrated that this mechanism in the human subject is essentially similar to that present in *Lepidosiren paradoxa*, and that in the human embryo there is a direct communication joining the sino-auricular node with the auriculo-ventricular node. The paper is to be submitted for publication in the *Journal of Anatomy*.

Dr F. DAVIES congratulated Dr Tudor Jones on his valuable work and suggested that the connection between sinu-auricular and auriculo-ventricular nodes described by Dr Jones may possibly be only transient. He referred to Shaner's observations on the transience of the interatrial node in the calf embryo, and to the fact that the connection described by Dr Jones had the character of "nodal tissue" in which the rate of conduction of the impulse is known to be much less than in ordinary cardiac (auricular) muscle, whereas Eyster and Meek had observed experimentally that the impulse commencing at the S.A. node reaches the A.V. node before the body of the auricle. Dr DAVIES also noted that it was remarkable that Dr Jones had found "cardiac nerves" in the heart of *Lepidosiren paradoxa* in every site in which specialised muscle had been described in every type of vertebrate heart, and wondered if Dr Jones would find specialised muscle in these sites at a later date.

Professor WALMSLEY, Professor BLAIR, Professor WILSON and Professor WOOLLARD also joined in the discussion.

Dr P. R. MACDONALD and Professor J. BEATTIE communicated a paper on "The innervation of the lachrymal gland."

The "parasympathetic" nerve supply to the gland is distributed to the glandular elements and does not seem to be associated with the excretory ducts. The "sympathetic" nerves are distributed entirely to the excretory ducts and blood vessels. The glandular elements are arranged in alveoli and as a secretory lining to the terminal portions of the ducts. These secretory ducts show large granules staining with acid fuchsin. The nerve fibres penetrate the cell membrane and ramify within the protoplasm ending finally on the nucleolar membrane. In the alveoli which do not show granules the intracellular loops are short and show more of the varicosities displayed by those in the cells of the secretory ducts. The loops end on the nucleolar membrane. The character of the endings and the granular arrangement suggest different functional divisions of the gland. The alveoli can be made to secrete by pilocarpine while the secretory granules in the ducts are discharged by acetyl choline.

The PRESIDENT congratulated the authors of the paper in having solved the problem of the nerve supply of the lachrymal gland! He also remarked with reference to the secretion of the tears that Nature has provided a very effective method of dealing with external wounds of the cornea by means of a saline solution.

Professor J. P. HILL enquired whether Professor Beattie had extended his observations to the nature of the secretion of the Harderian gland.

Professor BEATTIE in reply said that he had the impression that the

secretion of the Harderian gland was very similar to that of the lachryma. The lachrymal secretion normally has the power of inhibiting the growth of bacteria, after the parasympathetic nerve supply has been divided this action on bacteria is not present.

Professor LE GROS CLARK read a paper on "Experimental observations on thalamic connections in the rat." Lesions were produced in small localised regions of the cortex and in the thalamus, and the resulting Marchi degeneration was studied. The general conclusion was reached that all the principal nuclei of the thalamus in the rat with the exception of the antero-medial nucleus, the nucleus medialis ventralis and the mid-line nuclei, are related to cortical areas by reciprocal fibre connections. Special attention was called to the clear evidence of a direct fibre relation between the antero-ventral nucleus and the cingular area of the neopallium, and between the dorso-medial nucleus (nucleus medialis dorsalis, nucleus medialis *a*, nucleus medialis, of other authors) and the frontal pole of the neopallium.

Professor WOOLLARD, Professor WILSON and Professor LUCAS KEENE discussed the paper, Professor WILSON remarking that recent work has to a large extent done away with the significance of the term Optic Thalamus, which is now known not to be concerned with vision, and he suggested that the adjective "optic" should no longer be retained.

Professor H. H. WOOLLARD and Dr E. A. CARMICHAEL communicated a paper on "Some observations on alcohol injection of the fifth nerve."

This method of treating trigeminal neuralgia has been condemned by some surgeons in violent terms, but the observations we have made show that it is possible to produce complete anaesthesia of the area innervated by the fifth nerve, of long duration and without any complications whatsoever. The desensitised area corresponds in detail with the anatomical results obtained by removal of the Gasserian ganglion.

Dissociation of anaesthesia occurred only occasionally and then the area of loss of sensation of "prick" was often more extensive than loss to touch.

Recession of the area of anaesthesia when observed always occurred at the posterior or inferior margins of the anaesthetic area. This renders improbable the suggestion that the recession is due to ingrowth of fibres from adjacent areas.

Headache may occur and be referred to the anaesthetic area. Therefore all headaches are not due to tension on the dura. Some are generated centrally and referred to the periphery.

The study of such reflexes as the oculocardiac led to the belief, in association with other findings and the observations of other investigators, that the only function of the fifth nerve in the eyeball was the conduction of pain impulses.

Attempts were made to arouse pain by stimulation of the sympathetic plexus on the facial artery. No pain could be aroused, and this, taken in conjunction with the fact that teeth can be extracted and the eyeball enucleated after trigeminal anaesthesia has been induced, without producing pain, is against the notion that the sympathetic system may act as an accessory pain conduction path.

Taste was investigated and great variability discovered both in normal people and in treated cases of trigeminal neuralgia. Experimental injections

of post-mortem subjects revealed the fact that injected substances may pass into the posterior fossa along the central root and to the region of the geniculate ganglion by way of the hiatus Fallopii. The discrepancies about taste and our own observations suggest that taste in the anterior part of the tongue is normally often inactive and that most tasting is done by the region of the vallate papillae, and these are within the area innervated by the glossopharyngeal. An analysis by pressure with the algometer over various muscles, such as those innervated by the facial and those innervated by the motor root of the fifth and comparison with cases of facial nerve palsy and the like, led us to conclude that deep pressure pain fibres run in the facial nerve for the facial muscles and in the motor root of the fifth for the muscles of mastication.

Vasomotor changes do not occur after destruction of the Gasserian ganglion and there is no effect on salivation or lacrimation or on the co-ordination of eye movements. Blushing is equal on both sides of the face. A study of vascular reflexes with the thermopile and a study of facial palsy have led to the conclusion that the vasodilator nerves for the face run in the seventh nerve.

A study of the ganglion and the central root by anatomical methods has led to the conclusion that there is no complete segregation of fibres in the central root corresponding to epicritic and protopathic functions.

Professor LE GROS CLARK congratulated the authors on their demonstration of the degree to which it is possible to draw anatomical inferences from the study of clinical material which is so readily accessible in the wards of London hospitals. He enquired whether, in view of the suggestion which has repeatedly been made in recent years that the mesencephalic nucleus of the trigeminal nerve is the proprioceptive nucleus of the oculomotor muscles, any incoordination of ocular movements was to be observed after injection of the Gasserian ganglion or not. Professor WOOLLARD replied that no defect in ocular movements occurred after such an operation.

Professor ALEX. LOW made a communication on a specimen showing abnormal position of the thyroid gland. This communication will be submitted for publication in the *Journal of Anatomy*.

He also showed photographs and X-ray films of a case of full-time Thoracopagus twins.

Professor FRAZER in discussing Professor Low's first paper, said that the median thyroid had remained in its primary position. The lateral thyroids were in the position of the third pharyngeal pouches, not of the ultimobranchial bodies.

Professor R. D. LOCKHART gave a demonstration of "The acrobat in radiogram and cinema."

Acrobatic movements of the vertebral column and hip joint were discussed by photograph and radiogram. The still pictures were supplemented by 200 ft. of cinematographic film in ordinary and slow motion. The paper will be submitted for publication in the *Journal of Anatomy*.

Sir ARTHUR KEITH congratulated Professor Lockhart on the excellence and general interest of the demonstration, and said that there was much to be learned from X-ray photography. In addition to the movements of individual vertebrae, other movements were involved. In standing on one leg, the balancing movements involve all the muscles of the body, not one set only.

Professor FRAZER enquired whether the extreme degree of separation of

the bones at the sacro-iliac joint might not be explained by the direction in which the photograph was taken.

Mr HARRIS commented on the large number of elastic fibres which are present in the ligaments, and which permit elongation of these ligaments. In hyper-extension or bending backwards of the vertebral column there is a slipping downwards of the neural arch of the vertebra above on the articular processes of the vertebra below.

Professor LOCKHART in reply stated that in flexion of the vertebral column forwards, there was not only relaxation of the erector spinae, but controlled elongation or "paying out" of its fibres.

Dr MACDONALD CRITCHLEY communicated a paper on "The superior cerebellar artery."

Arising immediately before the bifurcation of the basilar, the superior cerebellar artery passes outwards just behind the third nerve. The artery divides at the most lateral point of the mid-brain into two branches which remain in close opposition with each other and also with the fourth nerve. Just lateral to the posterior corpus quadrigeminum, the two branches abruptly change their direction, looping first downwards and outwards and then outwards. The more lateral branch reaches the anterior margin of the cerebellum, sending twigs to the ala of the lobulus centralis and to the lobulus lunatus superior and inferior (*marginal*). Collateral branches supply the lateral aspect of the ventral pons (*middle peduncular*) and the flocculus (*floccular*). The mesial branch of the superior cerebellar artery gives off numerous twigs in the inter-quadrigeminal region which so anastomose with corresponding vessels from the opposite side as to form a complete circumpeduncular ring. The main part of the mesial branch passes on to the upper surface of the cerebellum and terminates in *vermicular* branches to the culmen, clivus and cacumen; and *lunate* branches to the whole of the upper surface of the cerebellum.

The territory of the superior cerebellar artery comprises: (1) a narrow transverse segment of the brain stem, within which are contained part of such structures as the red nucleus, the locus niger, brachium conjunctivum, oculo-motor nucleus, frontopontine and pyramidal pathways; and (2) the cortex and subjacent white matter of the upper surface of the cerebellum, including part of the dentate nucleus.

The superior cerebellar artery may be regarded from the standpoint of comparative anatomy as a composite vessel, formed by the union of two segmental vessels, the arteriae cerebelli α and β. We may perhaps regard the marginal branch—in part at least—as a vessel of some antiquity, being one of the nutrient vessels of the primitive flocculus. This branch is perhaps the homologue of the arteria cerebelli β. The mesial primary division of the human superior cerebellar artery possibly consists of a fusion of two vessels—an older (the vermicular) which probably represents the primitive arteria cerebelli α, and the more recent lunate branches associated with the expanding lateral masses of the cerebellum.

Professor ELLIOT SMITH remarked that the exact arterial supply of the cerebellum was a neglected field of anatomy. This distribution of the vessels raised points which were difficult to fit into any morphological scheme. According to Shellshear the dentate nucleus is supplied chiefly by the posterior inferior cerebellar artery; there is a large contribution, however, from the superior cerebellar artery. There is thus an overlap in the arterial supply of the

old and the new areas. The separation between the old and the new parts in the cerebellum is not so sharp as in the cerebrum.

Professor LE GROS CLARK suggested that the exact distribution of the vessels might be followed in thick sections of injected specimens using Professor Wilson's technique.

Mr A. T. HOPWOOD made a short communication on the "Age of Oldoway Man." The deposits in which the skeleton was found in 1913 consist of four beds of water-laid tuffs belonging to the Kamasian, or first Pluvial, period. They are numbered from below upwards as Beds I, II, III, IV. The skeleton was found very near to the top of Bed II, some 3–4 metres below the surface of the Serengetti plain.

Its position was such that it must either be very old, or else quite recent; either it is contemporary with the beds in which it was found, beds of Middle Pleistocene Age containing artefacts of a Chellean type, or else it is an intrusive burial of a modern native, i.e. a Masai.

The position of the skeleton on the right side is different from that adopted by the Masai, who always bury on the left side. Professor Reck, the discoverer, failed to find any trace of disturbance of the deposits, nor did he find any trace of stones having been used for a grave filling. The Masai always use stones to prevent the hyaenas abstracting the body. Hence it does not seem likely that the tribe was the modern Masai.

The Masai have inhabited the country for at least 250 years. At that time the hard overlying beds would have covered the spot where the skeleton lay. These beds are so hard that it would not be possible for a tribe armed only with native tools to sink a shaft 3–4 metres deep from the plain to make a burial at the bottom.

Those who visited the locality came to the following conclusions: (*a*) the skeleton is not Masai, despite physical resemblances, (*b*) in pre-Masai days the spot where the skeleton was found was so far below the surface as to be inaccessible to natives, hence an intrusive burial would be impossible, (*c*) if (*a*) and (*b*) are true, then the skeleton must have been deposited in Bed II before the overlying strata were laid down, and in that sense is contemporary with Bed II.

Mr HOPWOOD also demonstrated some fossil bones of Miocene Primates discovered at Kenya.

Mr CECIL P. G. WAKELEY read a paper on the "Position of the vermiform appendix, as ascertained by an analysis of 10,000 cases," and the following table shows the positions of the appendix, and their relative frequency:

Position of appendix	No. of cases	Percentage
1. Anterior or pre-ileal	100	1·00
2. "Splenic," or post-ileal	40	0·40
3. "Pelvic," on psoas muscle, near or hanging over the brim of pelvis	3101	31·01
4. Sub-caecal, beneath the "caput caeci"	226	2·26
5. Post-caecal and retro-colic	6528	65·28
6. Ectopic	5	0·05

Sir ARTHUR KEITH—on behalf of Dr L. S. B. LEAKEY—showed fossil teeth of an anthropoid about the size of the chimpanzee—from lower Miocene deposits, Rusinga Island, Lake Victoria, Uganda.

Professor WILSON made communications on:

(1) The nature of the *ligamentum nuchae.*

(2) A method of demonstrating thick serial sections of embryos.

(3) The growth of the caudal end of the Müllerian duct and its relation to the Wolffian duct.

Dr A. B. APPLETON read a paper on "Acceleration of epiphyseal ossification."

Professor T. WALMSLEY communicated a paper on "The torsion of the femur," which will be submitted for publication in the *Journal of Anatomy.*

Professor ARTHUR KEITH said that X-ray photographs of the long bones of old and young people showed considerable variations, and that the form of the bone depends largely upon the carriage of the individual.

The PRESIDENT remarked that the bones should be regarded as plastic and yielding to strain and pressure, e.g. with regard to the distal end of the fifth metatarsal, the condyles instead of being side by side are frequently "swung" round.

Dr WADDINGTON and Dr WATERMAN, introduced by Professor R. H. HUNTER, communicated a paper on "Experiments in the development of the early rabbit embryo." The paper will be submitted for publication in the *Journal of Anatomy.*

The PRESIDENT commented on the development of a new technique in experimental embryology and the remarkable adaptability of Nature in overcoming changed conditions.

Professor J. BEATTIE read a paper on "The mesencephalic nucleus of the trigeminal nerve."

Section of the third nerve produces degeneration of certain large cells in the more cephalic part of the mesencephalic nucleus. Degenerative changes are visible at 48 hours, but these disappear within 10 days. The method of staining was Cajal's 6 A (chloral hydrate). The presence of "boutons termineaux" on the large cells demonstrates that the large cells must be regarded as primary neurones.

Professor J. BEATTIE made a further communication on "Hypothalamic mechanisms."

Experimental and anatomical evidence was produced to show that there are at least two mechanisms within the hypothalamus. One of these—the posterior—is associated with the sympathetic nervous system. The other, which involves the anterior nuclei and the posterior lobe of the pituitary gland, is connected probably with parasympathetic centres. The afferent connections of the posterior division are mainly from the "fillet" nuclei of the thalamus while the anterior division receives afferents from anterior nuclei which in these have large cortico-thalamic components.

Professor ELLIOT SMITH remarked on the enormous importance of investigations on this part of the brain. Wide comparative studies in lower animals have shown that this region is almost as highly developed in them as in Man. He also commented on the important part played by appetites in connection

with nervous control. He considered this recent experimental work on the functions of the hypothalamic region to be a brilliant achievement.

Professor WILSON and Professor HILL also took part in the discussion.

Dr C. P. MARTIN read papers on (1) "Torsion of the head of the humerus" and (2) "The notch on the anterior edge of the glenoid fossa of the scapula." These will be submitted for publication in the *Journal of Anatomy*.

Professor FRAZER remarked that the notch on the anterior border of the glenoid fossa is present in a two-months' human foetus, before definite movements of the arm take place.

Professor ELLIOT SMITH said that torsion of the head of both the femur and the humerus was a human attribute, and due to changes in the position of the body.

Professor WALMSLEY regarded the changes in form of the long bones as of great importance from the evolutionary standpoint.

Professor WRIGHT compared the leaflet of synovial membrane which is in relation to the glenoid cavity with the fold of synovial membrane covering the Haversian body in the hip-joint.

Dr MARTIN, in reply to Professor Frazer's comment on the development of the notch before the subscapular tendon occupies it, said that this was not antagonistic to the explanation which he had given as there are numerous instances of structures making their appearance before they become functional.

Dr A. J. E. CAVE communicated a paper on "Nuclear erosions of the vertebral bodies," of which the following is an abstract:

In the lower dorsal and the lumbar, though never in the cervical, region the cranial and caudal surfaces of the vertebral bodies very frequently manifest curious erosion of their spongiosa in the form of pits, depressions or excavations. Though sometimes multiple, these erosions are usually single and are situated primarily at a point corresponding to the junction of the posterior third with the anterior two-thirds of the ventro-dorsal diameter of the vertebral surface concerned, i.e. situated immediately below (or above) the nucleus pulposus of the adjacent inter-vertebral disc. The depth of the erosions varies considerably in different specimens, the average depth being from 2 to 6 mm.: their outline exhibits great variety, being most frequently irregularly circular or crescentic, although bilobed, trefoil and various bizarre forms occur.

They are sufficiently common in the senile spine to be regarded as almost an inevitable age-change, but they may also be met with from adolescence onwards; at that age they were first detected by radiography in 1920 by Scheuermann (*Z. Orthop. Chir.* Bd. XLI) in kyphotic subjects.

Their mode of production with its great clinical significance has been made clear by the excellent anatomico-pathological studies of Schmorl of Dresden, working upon a hitherto unparalleled wealth of vertebral material, work admirably summarised by Beadle (*Med. Res. Coun. Spec. Rept.* No. 161, 1931). Schmorl has demonstrated that these erosions in the vertebral body spongiosa are produced by the prolapsed or herniated tissue of the nucleus pulposus, invading the vertebra through a defect in the cartilaginous disc plates, and occupying, in life, the excavation thus formed.

The intervertebral disc, in this connection, is regarded as a tripartite structure, comprising (*a*) the nucleus pulposus, (*b*) the annulus fibrosus *vel* lamellosus, and (*c*) the two thin plates of hyaline cartilage limiting the former

structures above and below and so intervening between the disc mass and the vertebral bodies. The extremely turgid nucleus exerts constantly great pressure on the cartilage plates; when, from any cause, this cartilage is ruptured there ensues escape of the nuclear tissue through the rent into the vertebral spongiosa with the consequent excavation thereof so evident in the macerated specimen.

The vertebrae here exhibited afford excellent examples of typical erosions.

Dr CAVE also read a paper on the "Significance of bifidity of cervical spinous processes," which will be submitted for publication in the *Journal of Anatomy*.

Dr J. D. BOYD read papers on (1) "Classification of the upper lip in Mammals," and (2) "The suckling mechanism in *Didelphys Virginiana*."

Dr BOYD classified mammals into five distinct groups according to differences in the relationships of the frontonasal process.

Professor FRAZER, speaking from the standpoint of human development, said that the development of the upper lip was a long process. The development begins early but is not completed until a late period. He enquired whether Dr Boyd had investigated the nerve supply of the central part of the upper lip.

Professor HILL, speaking with reference to the suckling mechanism in *Didelphys*, asked whether the young had not already become attached to the nipple. The fusion of the lips is not complete in the young at birth. The mother's nipple is attenuated at its extremity, and the lips form a complete circular collar surrounding the nipple.

Dr HENDERSON was inclined to think that the nerve supply of the central part of the upper lip was the nasopalatine. The under surface of the lip in its central part probably retains its original nerve supply from the nasopalatine. Anaesthesia of this region is increased by injection of the anaesthetic solution in the neighbourhood of the incisor teeth.

Dr HUNTER demonstrated a series of sections from a number of animal forms to show the presence of masses of ganglionic tissue situated between the longitudinal and circular muscles of the bowel at the ileo-caecal, caeco-appendicular, and caeco-colic junctions. He drew attention to the considerable differences in the relative amounts of matrix in each mass in different types of animal, and to the variation in the presence or absence of a capsule to each mass. It was suggested that these masses represent a modified form of Auerbach's plexus.

Dr F. DAVIES disagreed with Dr Hunter's view that the tissue described by Dr Hunter as nodal tissue had the true characters of nodal tissue. In cardiac nodal tissue the muscular element is predominant, whereas in the tissue described by Dr Hunter ganglionic elements are the main feature.

Dr J. B. BAXTER read a paper on the "Development of the vagina in the rabbit." This will be submitted for publication in the *Journal of Anatomy*.

Professor WILSON asked whether Dr Baxter had examined this region in Ungulates. In the cow the patent ducts of Gärtner lay alongside the vagina.

Professor FRAZER said that mistaken views had arisen in the past with respect to the development of the vagina in the human subject which were due

to the application of conditions found in lower animals to human development. Considerable modifications may occur more especially with regard to the lower ends of the Wolffian ducts.

Dr BAXTER, in reply to Professor Wilson, said that he had not investigated the development of the vagina in Ungulates.

DEMONSTRATIONS

Dr T. NICOL. "Abnormal early development of Cavia."

Dr D. J. HURRELL gave a demonstration of the "Vascularisation of cartilage." Five sections were shown through the foetal tarsus (C.R. lengths 9–21·7 cm.), showing the relative vascularity of the cartilages from its commencement to the start of ossification in the talus and os calcis.

Professor D. M. BLAIR and Dr F. DAVIES gave a demonstration of "Nerve elements in the conducting system of the heart."

Specimens from the cow's heart, prepared by a modification of Ranson's technique, showed the presence of nerve cells and of abundant nerve fibres in the auriculo-ventricular bundle and in its right and left limbs. Some of the finer relationships between the nerve fibres and the Purkinje muscle fibres were also demonstrated.

Dr W. F. HARPER gave the three following demonstrations.

(1) "Congenital atresia of the ileum."

This specimen demonstrates a complete atresia of the ileum, fully one inch long, and situated about two feet proximal to the ileocolic-orifice, at a site corresponding to the normal attachment of the vitello-intestinal duct. It is not possible even under pressure to force liquid through the stricture. Unfortunately, on account of technical difficulties, microscopic sections have not been made. The ileum proximal to the site of the obstruction is distended, while distally it is collapsed.

Clinical note. After birth, the child did not pass meconium and had persistent vomiting. An imperforate anus was suspected by the surgeon who performed a caecostomy. The child died seven days after birth. Post-mortem examination revealed no other abnormality than the one described.

Remarks. Numerous examples of congenital atresia of the ileum are on record, but in the majority of cases these are found much higher than the one demonstrated, are less in extent and generally give rise to only partial occlusion of the lumen. The position of the obstruction in the present case suggests that it may be caused by an over extension of the process associated with the normal obliteration of the vitello-intestinal duct.

I am indebted to D. F. Cappell, Professor of Pathology in the University of St Andrews, for permission to demonstrate this specimen.

(2) "Extensive melanism in the skeleton of *Raia Maculata*."

The specimen, a mature male, was caught in the North Sea, off Aberdeen. Every portion of the skeleton contained a deposit of melanin pigment. The deposit was heaviest in the vertebral column and the main cartilages of the

pectoral and pelvic girdles, where it imparted a coal-black colour to the skeleton, standing out in marked contrast to the white muscle masses. It was less marked in the terminal portions of the radialia of the fins, where it showed up brownish yellow. The pigment was confined to the cartilaginous skeleton only, and there was no evidence of invasion of myotomes or connective tissue septa. The skeleton, apart from the pigmentation, was normal and there was nothing unusual in regard to the normal skin pigmentation of the species. The skin itself was more fatty than usual, also the sub-cutaneous, intermuscular and peritoneal fat was increased in amount, but there was no evidence of any inflammatory process or tumour formation in the fish. The pigment is very stable, resisting the usual treatment of the tissues in the process of making microscopic sections. In the latter, the pigment granules appear in clumps scattered irregularly in the matrix surrounding the cartilage cells.

Chemical examination of the pigment.

The pigment was extracted from minced cartilage by boiling with methyl alcohol acidified with hydrochloric acid.

This solution after filtration showed no absorption bands. Treated with methyl alcohol holding HCl gas under reflux, it did not yield a methyl ester nor did it show any absorption bands. This definitely excludes all compounds of the porphyrin class, and, in particular, uroporphyrin, the pigment in ochronosis.

If the methyl solution of the pigment be mixed with hydrogen peroxide and exposed to light, the colour is completely discharged. This test would indicate that the pigment belongs to the group of "melanins."

Chemical analysis thus proves the pigment to be different from that found in ochronosis in the human subject, a rare condition in which cartilages, capsules of joints and other soft tissues become a dark brown or almost black colour, owing to the deposit of a pigment. In a certain proportion of cases of ochronosis, alkaptonuria has been present, a condition in which homogentisic acid is present in the urine; this substance is formed from aromatic compounds such as tyrosine, there apparently being in alkaptonurics an inability to break up the benzine ring in these substances. In some of these cases the aromatic compounds become oxidised into pigments which are deposited in the tissues producing the ochronosis. Like ochronosis, however, this extensive melanism in *Raia* appears to be the result of some general metabolic disturbance. Further than this, nothing can be said as to its genesis or significance.

Black pigment exists normally in most fishes, mainly in the chromatophores of the colour patterns. Massive deposits, however, are exceedingly rare, but have been recorded by Johnstone, in sarcomatous tumours of rays and other fishes. It has also been observed in the gills and liver of fishes having black-pigmented sarcomata of the skin and muscles. Johnstone has also recorded a case of extensive melanism in a herring, but in his specimen the pigment was contained in the muscles and in the connective tissue septa, the skeleton being free from pigment. I can find no record in the literature of a condition similar to the above in which the pigment is associated with the skeletal elements only. Detailed chemical examination of the pigment is lacking in previously recorded cases.

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—— (*b*) "Melanotic angiosarcoma in a plaice." *Report on Lancashire Sea-fisheries*, vol. XXXIII, p. 135.

(3) The communication on "Supernumerary pectoral fins in *Raia circularis* Loudon" will be submitted for publication in the *Journal of Anatomy*.

Professor J. BEATTIE showed slides demonstrating his "Cytological studies on the third nerve nucleus and the mesencephalic nucleus of the fifth nerve after section of the third nerve."

Dr H. L. GREEN demonstrated on "Brain sections stained by Mulligan's method."

ON THE CONNECTIONS OF THE ANTERIOR NUCLEUS OF THE THALAMUS

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In 1909, Sachs (6) published the results of his experimental investigation on the connections of the thalamic nuclei in the cat and the monkey. He stated that the anterior nucleus (his nucleus dorsalis magnus) sends off no fibres to the cerebral cortex, but is related by thalamic radiations with the head of the caudate nucleus. This conclusion has been generally accepted, although several observers—on the basis of normal Weigert material—have expressed the opinion that the anterior nucleus does give off corticipetal fibres. Recently, Glorieux (3) has reported findings similar to those of Sachs as the result of employing the Marchi method on the dog's brain. One of us, however, has found in the rat's brain definite evidence of a reciprocal fibre connection between the antero-ventral nucleus of the thalamus and the cingular areas of the neopallium (2). Since this result is in conflict with the usually accepted view, we have thought it desirable to investigate the matter in more detail.

METHODS

Our first aim was to produce a localised lesion in the anterior nucleus of the cat's thalamus in order to follow out the ensuing Marchi degeneration. For this purpose we used a Clarke-Horsley stereotaxic instrument, for the loan of which we are indebted to the British Association. We also wish to thank Mr Barrington, of University College Hospital, for so kindly giving us personal instruction in the use of this instrument.

By means of the Clarke-Horsley apparatus it is possible with the minimal error to produce electrolytic lesions in the thalamus without either serious injury to the cat or so damaging the surrounding brain as to interfere with the study of the material at a later date. We have for some time been concerned with a study by this means of the medially situated nuclei of the thalamus. In one of our experiments, a particularly favourable lesion was produced in the anterior nucleus, and a report of this case is given under section A of this paper. Histological sections were prepared by the usual Marchi technique.

Our next object was to produce lesions in the cingular areas of the cortex with a view to studying cellular atrophy in the thalamus some months after the operation. This we did with the brains of four rats and three cats. In the former, reported under section B of this paper, an incision was made (under ether anaesthesia) with a discission needle through the dorsal margin of the cerebral hemisphere in order to sever the fibres of the centrum ovale which are connected with the cingular cortex. One of these experiments was discarded,

as it was found later that the lesion had extended too deeply, reaching the dorsal surface of the thalamus itself. The rats were killed approximately 3 months after operation. The brains were embedded in paraffin, cut in serial sections and stained with Borell's methylene blue. The precise extent of the direct cortical injury was ascertained by a study of the serial sections and, moreover, it was found that the methylene blue had stained the course of the degenerated fibres which had been severed by the lesion, contrasting them in this way with the normal unstained white matter (see Plate IV, fig. 1, and Plate V). By reference to these points, the areas of the cortex which had been cut off from the thalamus could be fairly accurately delineated, and they are shown diagrammatically in text-fig. 3.

In section C of this paper, a report is given of experiments on three cats in which cortical lesions were made in a corresponding position. Under ether anaesthesia the fronto-parietal area of the cortex was exposed on the right side and an incision made with a tenotome into the cingular gyrus so as to cut off the connections of this area with the thalamus. The animals were killed approximately 4 months after the operation. In each case, the thalamus was sectioned serially and stained with Borell's methylene blue.

The nomenclature of the thalamic nuclei is that employed by one of us in a paper published recently in *Brain* (1). With regard to the cerebral cortex of the cat, the nomenclature of Winkler and Potter's classical atlas (7) is used for the reason that this atlas is readily accessible to other workers.

A

Cat No. 8

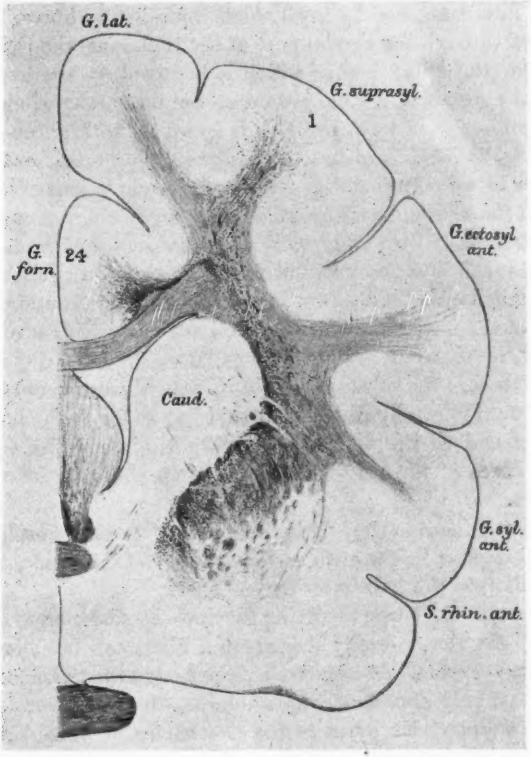
The operation was performed under ether anaesthesia on 14 April, 1932. A vertical mid-line incision was made from the external occipital protuberance downwards for a convenient distance and the bone over the right cerebellar hemisphere freely removed. The Clarke-Horsley apparatus was next applied and the bipolar electrode inserted through the opening in the skull to a point 12 mm. anterior to the central point, 2 mm. above the horizontal plane and 1·5 mm. to the right of the sagittal plane (instrumental error was allowed for). A current of 5 milliamps was allowed to flow for 5 min., after which the apparatus was removed and the wound closed. The cat was killed on 3 May, 1932.

Examination of serial sections

The electrolytic lesion was found to be in the rostral end of the dorsal part of the thalamus, involving the anterior nucleus (antero-ventral and antero-medial elements), the frontal end of the dorso-medial nucleus, the extreme antero-medial portion of the ventral nucleus (n. ventralis pars anterior of Rioch (4)), and the upper end of the inferior peduncle of the thalamus. The size and position of the lesion may be readily apprehended by reference to Plate I, fig. 1. It extends forwards horizontally to a point immediately lateral to the descending column of the fornix. The lesion is confined to the thalamus and

does not involve the internal capsule at all. The lateral nucleus is uninjured and is entirely free of osmic deposit at the rostral thalamic levels.

From the site of the lesion in the anterior nucleus, fasciculi filled with fine Marchi granules run in great numbers through the stratum subcaudatum to reach the internal capsule. They can be traced in continuity forwards and laterally, and then pass dorsally in relation to the anterior callosal fibres. Still



Text-fig. 1. Frontal section through the right hemisphere of Cat No. 8 at a level just rostral to the position of the electrolytic lesion in the thalamus. For description, see text. The numbers in this and the next text-figure indicate the position of Brodmann's cortical areas. × 4.

more rostrally, at the level of the septal region, they turn abruptly medially and run along the dorsal surface of the corpus callosum to reach the gyrus fornicatus (cingular gyrus) (see text-fig. 1). In this position, the degenerated fibres form a bundle which runs caudally, distributing to the whole length of the cingular gyrus, the grey cortex of which is scattered with fine osmic granules. This strip of cortex comprises the areae limbica anterior, posterior and retrolimbica. It should be noted that there is a complete absence of Marchi

deposit in the caudate nucleus and that the cingulum likewise contains no degenerated fibres.

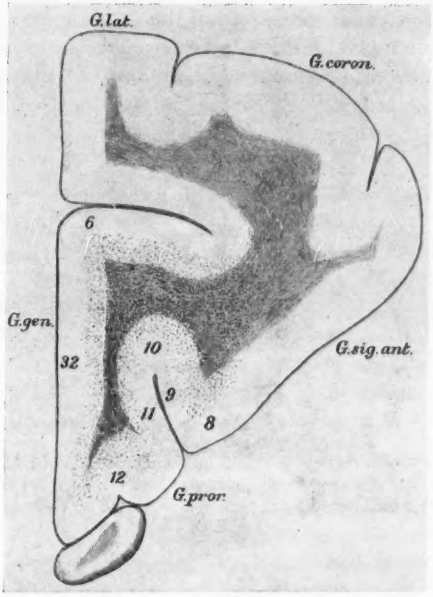
The lesion involves the commissura inter-antero-dorsalis on the right side of the mid-line, and Marchi granules are scattered throughout the fibres of the commissure and in the substance of the antero-dorsal nucleus of the opposite side. On the other hand, the antero-ventral and antero-medial nuclei of the left side are clear of osmic deposit. It thus appears that only the antero-dorsal elements are interconnected by myelinated commissural fibres.

In sections through the caudal part of the thalamus, the right mammillo-thalamic tract (the upper end of which is involved by the lesion at rostral levels) contains scattered Marchi granules. Similarly, the whole of the large medial mammillary nucleus of this side is sprinkled with a fine osmic deposit (see Plate I, fig. 2). This corroborates the observations made on the rat's brain with reference to a descending degeneration following lesions of the mammillo-thalamic tract (2) and would seem to indicate the presence of thalamo-mammillary fibres in the bundle of Vicq D'Azyr. The question of a retrograde degeneration must here be taken into account, but from a study of our sections we are inclined to the opinion that it does not account for this Marchi staining. The most medial part of the lesion involves the periventricular system of fibres in the dorsal part of the thalamus and, as a result, fasciculi of fine degenerated fibres can be traced up into the substance of the ipsilateral parataenial nucleus. They can also be traced ventrally close to the mid-line as far as the horizontal level of the medial end of the ventral medullary lamina of the thalamus. No degenerated fibres of the periventricular system could be followed into the hypothalamus.

The injury produced in the inferior peduncle of the thalamus has resulted in a rich Marchi deposit in the stria medullaris of the same side, which can be traced caudally into the habenular nucleus.

From the site of the lesion involving the dorso-medial margin of the nucleus ventralis pars anterior, coarsely degenerated fibres can be followed laterally into the internal capsule. At a level a little rostral to the lesion (see text-fig. 1), these fibres, not very abundant, run somewhat discretely through the white matter of the suprasylvian gyrus to the grey cortex of which they ultimately distribute (area post-centralis and area parietalis). Degenerated fibres in the subcortical white matter are only present in the anterior part of the gyrus. More caudally, at the level of the habenular ganglion, they are much fewer in number, and still more caudally they are limited to the grey cortex which contains osmic granules in its substance as far back as the sections have been taken i.e. to the transverse level of the medial geniculate body. The dorso-medial nucleus, as stated above, is involved directly by the lesion at its rostral end. More caudally, the track of the needle passes along the ventro-lateral margin of the nucleus, cutting across the fasciculi of the thalamic radiations which are connected with it. The nucleus itself is filled with Marchi deposit and degenerated fibres (containing fine osmic granules) course ventro-laterally

and take up a position in the most medially situated fasciculi of the internal capsule. Here they pass forwards lying close up against the ventro-lateral margin of the head of the caudate nucleus (see text-fig. 1). In sections taken through the frontal region of the hemisphere (see text-fig. 2), the medio-ventral part of the centrum ovale contains many degenerated fibres, and the distribution of Marchi granules indicates that they are destined to reach the cortex of the genual gyrus, the gyrus proreus, and the ventral lip of the anterior sigmoid



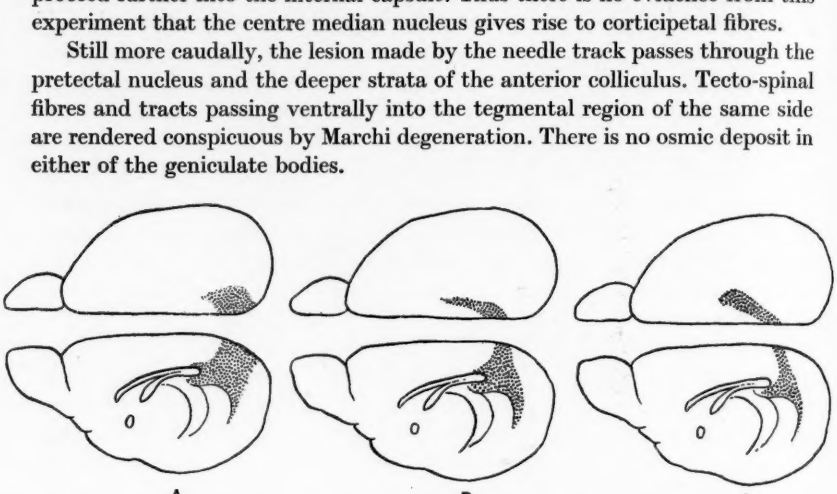
Text-fig. 2. Frontal section through the frontal region of the right hemisphere of Cat No. 8, showing the distribution of Marchi degeneration at this level in the white matter and the cortex. × 4.

gyrus. It is not possible from these sections to affirm the precise origin of these degenerated fibres, but, by reference to other experiments (2), it is probable that those which terminate in the genual gyrus (the area praelimbica) are derived from the lesion in the anterior nucleus, while those which terminate in the ventral part of the lateral surface of the frontal lobe (i.e. in areae frontalis granularis, praefrontalis, orbitalis lateralis, orbitalis intermedius, and orbitalis medialis) result from the involvement by the lesion of the dorso-medial nucleus and the thalamic radiations connected with it[1].

[1] Since writing this, we have studied the nuclear degeneration which follows on a lesion involving the frontal pole of the cerebral hemisphere in the cat. While in such a case there is marked cellular atrophy in the lateral portion of the nucleus dorso-medialis, the elements of the anterior nucleus remain intact.

In the caudal part of the thalamus, the track of the needle has cut through the upper end of the habenulo-peduncular tract and the nucleus parafascicularis, including the homologue of the centre median nucleus (see Rioch (5)). From the latter, fine degenerated fibres can be traced into the most medial part of the pars posterior and pars principalis of the lateral nucleus, but none proceed further into the internal capsule. Thus there is no evidence from this experiment that the centre median nucleus gives rise to corticipetal fibres.

Still more caudally, the lesion made by the needle track passes through the pretectal nucleus and the deeper strata of the anterior colliculus. Tecto-spinal fibres and tracts passing ventrally into the tegmental region of the same side are rendered conspicuous by Marchi degeneration. There is no osmic deposit in either of the geniculate bodies.



Text-fig. 3. Dorsal and medial views of the right hemisphere of A, Rat CC 1; B, Rat CC 3; and C, Rat CC 4. The extent of the neopallial cortex which has been injured or whose thalamo-cortical fibres have been severed by the lesion is indicated by the stippled area. × 2.

B

Rat (*Lab. No. CC* 1)

The dorsal margin of the right hemisphere had been incised longitudinally at a distance of 1·8 mm. from the mid-line, the incision reaching below into the medial surface of the cerebrum behind the corpus callosum at the upper margin of the hippocampus. The lesion extends forwards to the caudal extremity of the corpus callosum and back into the occipital pole, being confined to the cortex and subcortical white matter. From a study of the sections, it is apparent that the fibres in the centrum ovale which are related to the cingular areas caudal to the corpus callosum (area *z* of Fortuyn or 29 of Brodmann) as well as to the upper and medial half of the area striata have been severed (see text-fig. 3 A).

In the thalamus, the antero-ventral nucleus of the side of the lesion shows an atrophy of the cells in the dorsal third of its caudal half. These cells are shrunken, stain only lightly, and many have disappeared altogether (see Plate III B). The antero-dorsal and antero-medial elements are normal. The laterally situated cells of the dorsal nucleus of the lateral geniculate body also

show distinct atrophic changes. All the other thalamic nuclei, including the subdivisions of the lateral nucleus and the ventral nucleus, show no cellular change.

Rat (*CC* 3)

The lesion was a linear incision running backwards and slightly medially. At its anterior extremity it is 1·5 mm. from the mid-line at the level of the middle of the corpus callosum and at this level extending through the cortex into the subjacent white matter. Caudally, the lesion reaches the mid-line at the posterior margin of the hemisphere, cutting across the fibres of the centrum ovale which are connected with the caudal part of the callosal areas. The sections indicate also that a small part of the superior parietal region of the cortex is also involved. The lesion is confined to the cortex and centrum ovale (see text-figure 3 B).

In the thalamus, the cells in the dorsal quarter of the antero-ventral nucleus are shrunken and poorly staining, and diminished in density. A few scattered normal cells remain at the dorsal margin (see Plate III C). This atrophy extends almost to the rostral extremity of the nucleus. The antero-dorsal and antero-medial elements show no recognisable change. In the pars principalis of the lateral nucleus of the side of the lesion, some of the deeper cells in the rostral and medial part have undergone atrophy, but the greater part of this nucleus appears normal. The pars posterior of the lateral nucleus, the lateral geniculate body and the ventral nucleus are unchanged.

Rat (*CC* 4)

The anterior end of the lesion is situated 2·5 mm. from the mid-line at a level just behind the middle of the corpus callosum, involving here the fibres passing to the superior parietal area of the cortex but not reaching those connected with the callosal region (area limbica posterior). Caudally, the lesion is more medial, extending into the upper end of the hippocampal formation. The extent of the neopallial cortex which has been involved directly or indirectly by this lesion is indicated in text-fig. 3 C. As in the previous experiments, there is no injury to the basal ganglia.

In the thalamus, the antero-ventral nucleus shows an atrophy of the cells forming its dorsal and ventro-lateral margins. In addition, the cells towards the centre of the nucleus appear less dense, and many of them somewhat shrunken (see Plate III D). The antero-dorsal and antero-medial elements appear normal. The pars principalis of the lateral nucleus on the side of the lesion also shows definite degenerative changes, many of the cells—especially those situated medially and ventrally—having undergone marked atrophy to an extent which may be appreciated by reference to Plate IV, fig. 2. The pars posterior of the lateral nucleus, the ventral nucleus, and the lateral geniculate body present a normal appearance.

C

Cat (*Lab. No.* 9). *Operated upon* 19 *April, killed* 1 *September*, 1932

After the right fronto-parietal region had been exposed, a tenotome was used to make an incision approximately 12 mm. long and 6 mm. deep and at an angle of 30° to the vertical through the cingular gyrus. The wound in the scalp was then closed. Macroscopic examination showed that the lesion extends back from a point 18 mm. behind the crucial sulcus almost to the caudal extremity of the gyrus suprasylvius medius. Superficially the lesion is 7·5 mm. at its greatest width, reaching medially to 4·5 mm. from the mid-line, and appears to be limited to approximately the middle three-fifths of the gyrus suprasylvius medius and a corresponding extent of the lateral margin of the gyrus lateralis.

Sections of the hemisphere show that the injury also extends down into the white matter as far as the roof of the lateral ventricle, involving the fibres

Text-fig. 4. Frontal section of the dorsal part of the cerebrum of Cat No. 9, taken through the site of the lesion at its maximum width, at a level 11 mm. behind the anterior end of the corpus callosum. × 1½. *L.* gyrus lateralis; *Ss.* gyrus suprasylvius medius; *Es.* gyrus ectosylvius medius.

of the centrum ovale which are connected with the gyrus fornicatus, gyrus splenialis, and the upper lip of the gyrus ectosylvius medius. Moreover, the fibres which (as the first experiment recorded in this paper shows (Cat No. 8), course backwards along the dorsal surface of the corpus callosum to serve the caudal part of the cingular cortex, are destroyed at this level by the lesion (see text-fig. 4). The lesion nowhere extends beyond the cortex and subcortical white matter, i.e. the basal ganglia are quite intact.

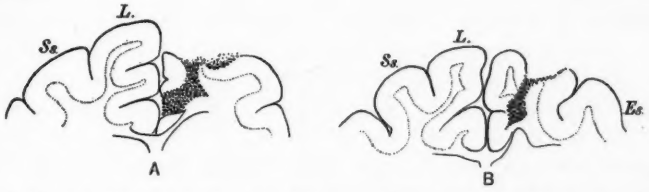
Examination of serial sections

The course of the degenerated fibres which have resulted from the cortical injury 4 months previous to death is indicated in the sections by the blue staining of the stratum subcaudatum (Plate V, A) of the injured side. The track of the degenerated fibres can in this way be traced ventro-medially into the medullary lamina lying between the antero-ventral nucleus and the ventral nucleus, pars anterior. The degenerative changes in the anterior nuclear group of the injured (right) side are very evident. The cells of the antero-ventral nucleus have for the most part disappeared, normal cells being represented by a very few only, which are scattered uniformly throughout the substance of the

nucleus (see Plate V). On the other hand, the antero-medial nucleus appears to be unaffected with the possible exception of a few cells along its ventro-lateral margin. The antero-dorsal nucleus of the injured side also shows a diminution of its cells which—on a rough computation and by comparison with the normal side—have been reduced by rather more than half their number.

The cells at the dorsal extremity and along the dorso-medial margin of the ventral nucleus, pars anterior, have mostly undergone complete degeneration, the few that remain in this position being small and atrophic. This degenerative process extends back to involve also the cells forming the rostral part of the nucleus centralis lateralis, an intralaminar nucleus which, as one of us has pointed out (1), is probably to be regarded in part as merely a marginal zone of the ventral nucleus whose cytoarchitecture has here been modified by fibres of passage.

The rostral part of the nucleus lateralis, pars principalis, is normal in appearance.



Text-fig. 5. Frontal section of the dorsal part of the cerebrum of Cat No. 10, showing the extent of the lesion at the level of A, the anterior end of the corpus callosum, and B, the junction of the middle and posterior thirds of the corpus callosum. × 1½. Lettering as in text-fig. 4.

Cat. No. 10. *Operated upon* 23 *April, killed* 5 *September,* 1932

The right fronto-parietal region of the cortex was exposed and an incision made with a tenotome at an angle of 35° to the vertical into what was considered to be the cingular gyrus over a distance of 13 mm. and for a depth of approximately 7 mm. The wound in the scalp was then sutured.

The lesion extends anteriorly to a point 5 mm. behind the crucial sulcus and runs directly backwards at 2–3 mm. from the mid-line along the lateral lip of the gyrus lateralis. Superficially, it appears to reach back approximately to the level of the middle of the gyrus suprasylvius medius, but, in sections, it is found to extend under the surface as far caudally as the posterior end of the corpus callosum. The sections shown in text-fig. 5 indicate that the lesion involves the gyrus lateralis and gyrus suprasylvius medius and the fibres of the centrum ovale connected with these, and that, at rostral levels, it encroaches on the cortex of the gyrus fornicatus without, however, damaging directly the fibres which pass to the caudal part of this gyrus. The lesion is limited to the cortex and the subcortical white matter.

Examination of serial sections

The blue staining shows the course of the degenerated fibres on the side of the lesion running through the stratum subcaudatum and in a ventro-medial direction into the thalamus, passing between the antero-ventral nucleus and the pars anterior of the ventral nucleus. There is some cell degeneration in the anterior nucleus, but not so marked as in the case of Cat No. 9. The atrophy affects mainly the caudal and ventral cells of the antero-ventral nucleus, but, in addition to this, there is a general thinning out of the cells throughout the nucleus as compared with the normal side. Most of the degenerated fibres run to the caudal end of the nucleus ventralis, pars anterior, and into the most dorsal margin of the pars arcuata at this level. Here there is a well-defined area in which the cells of the ventral nucleus have undergone extensive degeneration, and, as in the previous case, this cellular atrophy also affects the nucleus centralis lateralis in part. The pars principalis of the lateral nucleus is normal.

Text-fig. 6. Frontal section of the dorsal part of the cerebrum of Cat No. 11, showing the extent of the lesion, at the level of 7 mm. behind the anterior end of the corpus callosum. × 1½. Lettering as in text-fig. 4.

Cat No. 11. *Operated upon* 26 *April, killed* 5 *September,* 1932

After exposing the right fronto-parietal cortex, it was thought that an incision had been made 12 mm. long and 7 mm. deep at an angle of 35° to the medial aspect of the cerebral hemisphere. Subsequent examination showed the lesion to be quite superficial in extent.

Superficially the lesion is seen to be a sagittal incision confined to the gyrus lateralis and the dorsal lip of the gyrus suprasplenialis, extending back from the level of the ansate branch of the lateral sulcus almost to the caudal end of the gyrus lateralis, and reaching out to about 3 mm. from the mid-line. Sections of the hemisphere (see text-fig. 6) show that the lesion is quite superficial, injuring only the summit of the gyrus lateralis through approximately its middle third, and, to a very slight extent, the surface layer of the gyrus splenialis. The gyrus suprasylvius, gyrus fornicatus, and the fibres of the centrum ovale which are connected with them, are all intact.

Examination of serial sections

The anterior nuclear elements are quite normal, and there is no definite evidence of atrophy affecting the elements of the lateral, ventral, or other

thalamic nuclei. The results of this experiment are thus quite negative, but a record of it has been included here because it provides a control for comparison with the previous two experiments.

CONCLUSIONS

Our Marchi preparations of the brain of Cat No. 8 establish the fact that the anterior nucleus of the thalamus is related by corticipetal fibres with the whole length of the gyrus cingularis, and thus confirms previous observations made on the rat's brain (2). The complete absence in this material of any osmic deposit in the caudate nucleus leads us to the opinion that the statement that the anterior nucleus gives off medullated fibres to this nucleus is incorrect.

Following lesions in the cingular cortex of the cat and the rat, we have found cellular atrophy in the anterior nucleus. In the rat, this was confined to the dorsal and lateral part of the antero-ventral nucleus when the caudal part of the cingular areas had been involved, the antero-dorsal and antero-medial elements showing no recognisable change. In the cat, similar cortical lesions led to an atrophy of the antero-ventral nucleus in whole or in part, and to partial atrophy of the antero-dorsal nucleus. The antero-medial element in this animal remained unaffected, with the possible exception of cells situated along its ventro-lateral margin. It is possible that the antero-medial element is related rather to that part of the cingular cortex which extends on to the medial aspect of the frontal region of the hemisphere, a region of the cortex which was not injured in the experiments here reported. We are also in some doubt as to whether the nuclei which have been termed "antero-medial" in the thalamus of the cat and the rat are strictly homologous. The absence of apparent cell degeneration in the antero-dorsal nucleus of the rat in these experiments in comparison with the partial atrophy of this nucleus in the cat suggests that in the former the cortical lesions were less complete. The precise relation of the elements of the anterior nucleus to different subdivisions of the cingular area of the cortex requires a further and more detailed experimental enquiry. The presence of a descending Marchi degeneration in the mammillo-thalamic tract following a lesion of its upper end (in Cat No. 8) indicates the existence of a thalamo-mammillary component in this bundle. Our experiments have also shown that in the cat, the cortex of the gyrus suprasylvius medius receives fibres from the dorsal extremity and dorso-medial margin of the nucleus ventralis, pars anterior, the dorso-medial margin of the rostral part of the nucleus ventralis, pars arcuata, as well as from the rostral part of the nucleus centralis lateralis (which we believe to be, in part at least, merely the peripheral zone in this position of the nucleus ventralis itself). Further, in the rat (as shown by experiment CC 4) the lateral nucleus, pars principalis is related by corticipetal fibres with the most dorsal part of the posterior parietal region of the neopallium, a conclusion which was reached by one of us on the basis of Marchi degeneration (2).

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EXPLANATION OF PLATES

Plate I

Fig. 1. Frontal section through the rostral part of the thalamus of Cat No. 8, showing the position of the electrolytic lesion. × 8·5. *Ad.* antero-dorsal nucleus; *Av.* antero-ventral nucleus; *Am.* antero-medial nucleus; *La.* lateral nucleus, pars principalis; *Dm.* rostral end of dorso-medial nucleus; *Va.* rostral end of nucleus ventralis, pars anterior; *Vm.* rostral end of nucleus ventralis, pars medialis.

Fig. 2. Frontal section through the mammillary bodies of Cat No. 8, showing Marchi degeneration in the terminal fasciculi of the right mammillo-thalamic tract and in the substance of the mammillary body of the right side, following a lesion which involves the upper end of the ipsilateral mammillo-thalamic tract. × 30.

Plate II

Frontal section through the caudal part of the corpus callosum and cingular gyri of Cat No. 8, showing Marchi degeneration in the gyrus on the right side following a lesion of the anterior nucleus of the same side of the thalamus. × 20.

Plate III

Frontal sections of the anterior nucleus of A, normal rat; B, Rat CC1; C, Rat CC3; D, Rat CC4. In the last three cases, the caudal portion of the cingular cortex has been involved by a lesion and a corresponding cellular atrophy in the dorsal part of the antero-ventral nucleus may be noted. × 52. *Ad.* antero-dorsal nucleus; *Av,* antero-ventral nucleus; *Am.* antero-medial nucleus; *Sm.* stria medullaris; *V.* ventral nucleus.

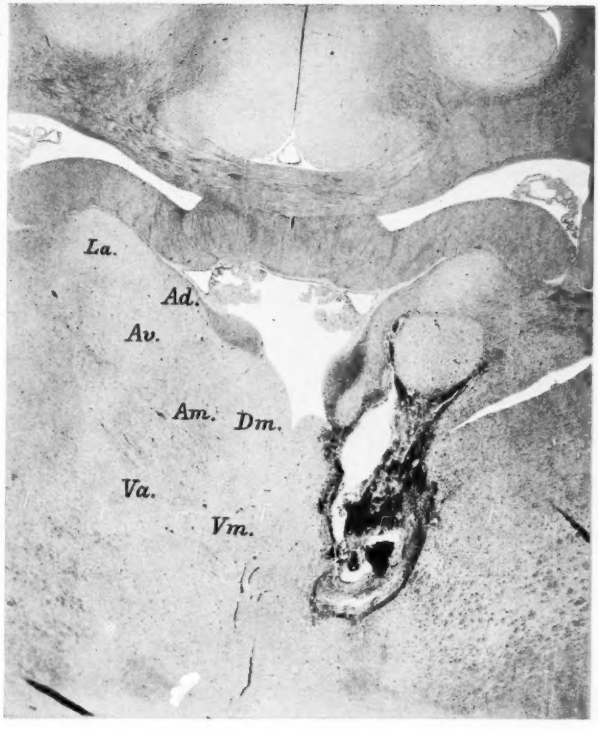
Plate IV

Fig. 1. Frontal section of the dorsal margin of the cortex of Rat CC 3 through the anterior part of the lesion (compare text-fig. 3 B). The lesion can be seen penetrating the cortex at the medial margin of the area striata. The arrow points to a leash of degenerated fibres from the cortical area involved, the course of which is marked out by staining with methylene blue. × 27.

Fig. 2. Frontal sections of the lateral nucleus (pars principalis) of the thalamus of rat CC 4, of the left (A) and right (B) sides. Note the cell atrophy in the right nucleus, following on a lesion involving the superior parietal area of the cortex (compare text-fig. 3 C). × 40.

Plate V

Frontal section through the anterior nuclei of the thalamus of Cat No. 9. × 12. Note that the antero-ventral nucleus on the side of the lesion has almost disappeared. The right side of the thalamus is to the left side of the figure, *a.* course of degenerated fibres following the cortical lesion, marked out by methylene blue staining; *Ad.* antero-dorsal nucleus; *Av.* antero-ventral nucleus; *Am.* antero-medial nucleus; *La.* nucleus lateralis, pars principalis; *Va.* nucleus ventralis, pars anterior; *V.arc.* pars arcuata; *Vm.* pars medialis.



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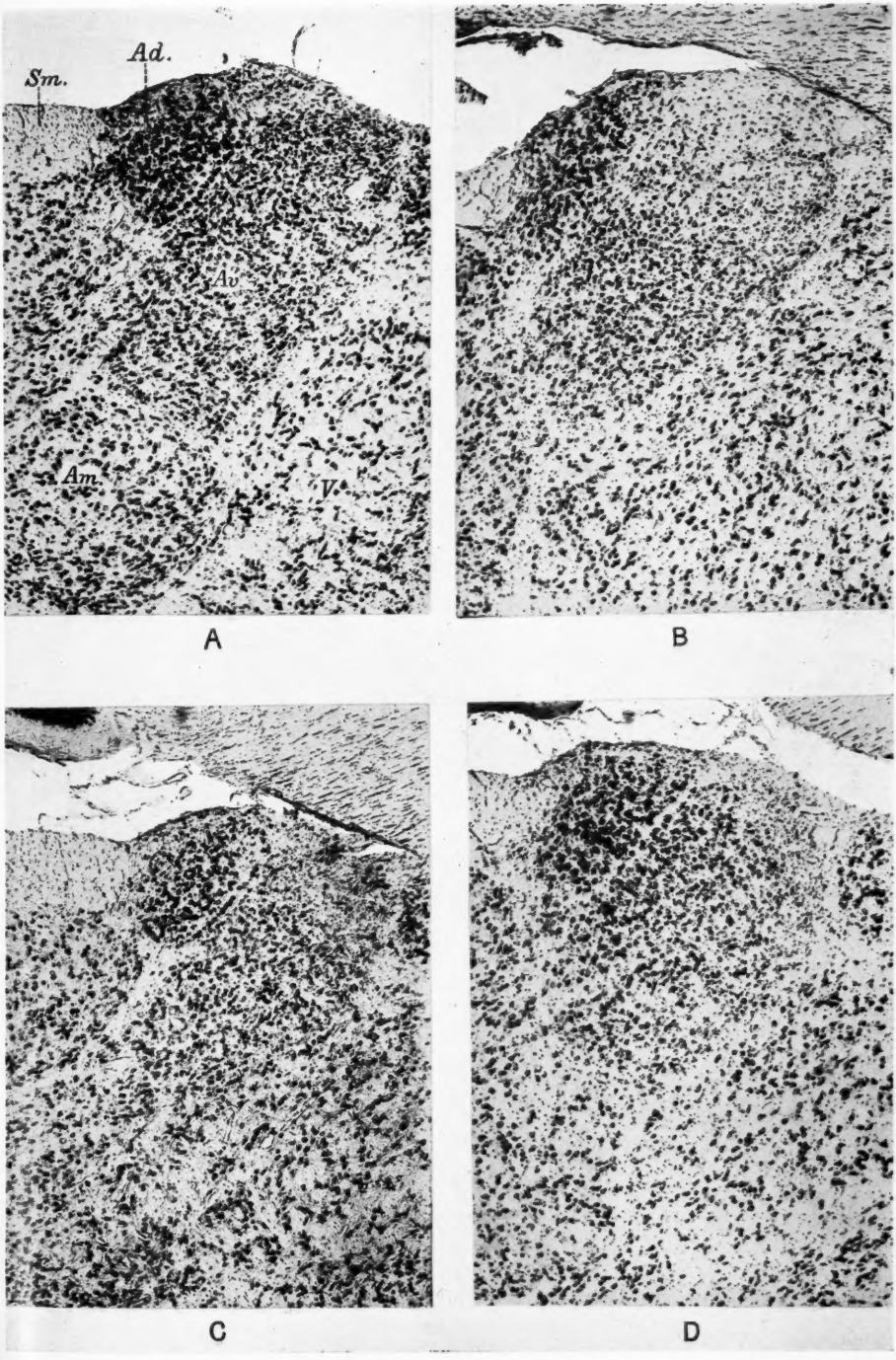
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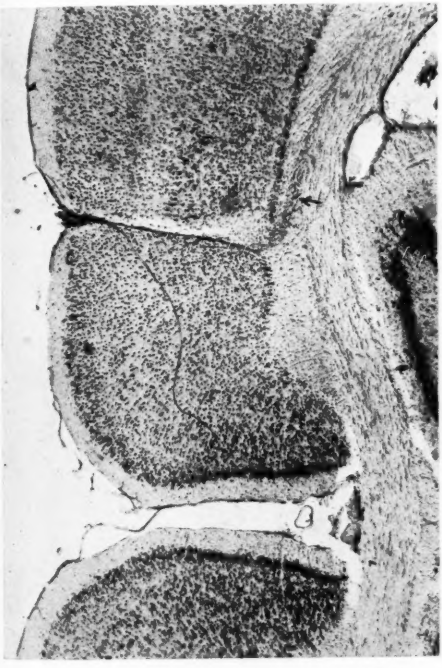

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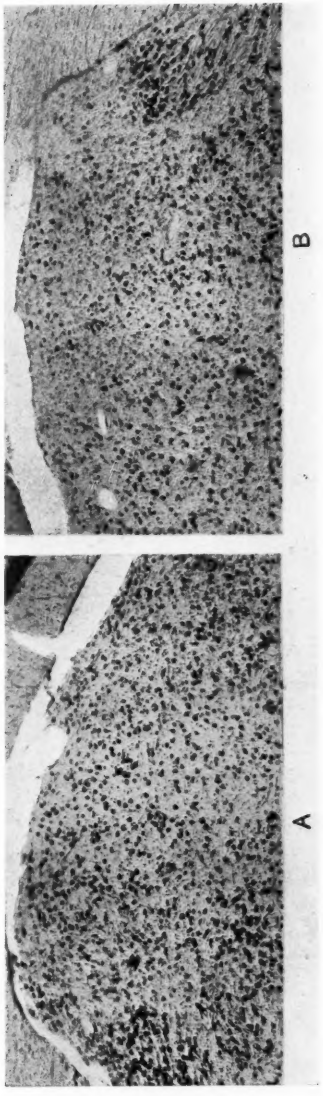

Fig. 2.

Lá.
Ad.
Ad.
Va.
Varc.
Am.
Vm.
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HYPOPHYSIO-PORTAL VESSELS AND THEIR COLLOID ACCOMPANIMENT

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At the meeting of the Anatomical Society of Great Britain and Ireland held at University College, London, on 30 June, 1930, we called attention to the presence of a peculiar (and until then unrecorded) system of vessels in the stalk of the pituitary (Proceedings of the Anatomical Society, *J. Anat.* vol. LXV, p. 178). Subsequently a short note was published in *The Lancet* (2 August, 1930, p. 238) and another in *The Journal of Anatomy* (October, 1930, pp. 88–91). In these preliminary communications we gave only the bare facts concerning these vessels without microphotographs, the slides having been shown at the Anatomical Meeting on 20 June.

We wish now to make a third communication for two reasons:

(1) To clear up some misunderstandings by giving microphotographs of the hypophysio-portal vessels to demonstrate the presence of colloid in the lumen and to show the course of these vessels as seen in serial sections, and

(2) To draw attention to the statements of previous observers concerning these vessels and in particular to the memoir of Karl Pietsch (of the Pathological Institute of the University of Jena), "Aufbau und Entwicklung der Pars tuberalis des menschlichen Hirnanhangs in ihren Beziehungen zu den übrigen Hypophysenteilen" (*Zeitschrift für mikrosk.-anat. Forschung*, 1930, Bd. XXII, S. 227–56).

The manuscript of his paper was sent to the *Zeitschrift* on 4 June, 1930, 16 days before we, in ignorance of his work, reported to the Anatomical Society the results of the work upon which we had then been engaged for about a year. It was not until June, 1932, that Pietsch's paper was brought to our notice. He had observed the vessels which we call hypophysio-portal, but he did not pursue them into the secondary net. He says (*op. cit.* p. 232): "Die Struktur der Pars tuberalis wird wesentlich bestimmt durch auffallend reichliche und weite Blutgefässe sowie durch ein kräftig entwickeltes Bindegewebsgerüst. Stellenweise nehmen die meist strotzend gefüllten Blutgefässe fast die ganz Dicke der Pars tuberalis ein,...die Gefässe zum grossen Teil für die Pars tuberalis keine funktionelle Bedeutung haben, sondern nur ihren Weg durch sie hindurchnehmen," p. 233. "Die Venen und die Kapillaren der Pars tuberalis stammen aus dem Vorderlappen...*zum Teil sollen sie in den Sinus*

circularis münden, zu einem grossen Teil sehe ich sie aber auf meinen Schnitten in das Innere des Stiels übertreten und diesem tuberwärts ziehen." Italics ours.

These are the hypophysio-portal vessels of our account. Pietsch also observed colloid in these vessels. He says (*loc. cit.* p. 233): "Da es morphologische (Kolloid in den Gefässen) und pharmakologische (Hypophysingehalt des Venenblutes) Anhaltspunkte dafür gibt dass das Vorderlappensekret zum Teil durch die Gefässe abgeführt wird, könnte man aus den Eindringen der Venen in den Stiel und in das Tuber cinereum vermuten dass nicht bloss die Saftspalten des gliösen Stiels für den Sekretstrom von Vorderlappen zu den hypothalamischen Zentren in Betracht kommen, sondern auch der Gefässweg."

What was for Pietsch an interesting subsidiary observation has been for us the basis of the histological work we have already communicated and of a considerable amount of experimental work not yet published.

We regard Pietsch's work and our own as being clearly confirmatory the one of the other in this matter of a venous drainage from the hypophysis to the hypothalamic region, the observations individually recorded being entirely independent the one of the other.

In our short notes published in 1930, we stated the fact that there is a system of veins taking origin from the sinusoids of the buccal portion of the hypophysis and from the capillaries of the neural portion, which ascend through the stalk to the region of the floor of the infundibular recess of the 3rd ventricle where they break up into a secondary capillary net. As they ascend, these run first in the substance of the pars tuberalis, mostly in front of the stalk, and then at various levels penetrate into the neural portion of the stalk and ascend within "glial sleeves" towards the floor of the infundibular recess, where they lose their glial wrapping and break up into the secondary net.

That the blood flows in these vessels in the direction stated is evident from their colloid accompaniment. As colloid—whatever it may be—is formed in the pituitary and not in the brain, its association with the vessels may be taken as indicating that the direction of the flow is certainly hypophysio-hypothalamic. Sometimes colloid globules occur within the lumina of these vessels, sometimes in the intervascular tissue of the neural portion of the stalk, and sometimes in the vicinity of the secondary net.

Plate I, fig. 1 is a microphotograph of a frontal section through the hypophysis and its stalk, stained with haematoxylin and eosin.

From the anterior lobe of the hypophysis one can see a large sinusoid being continued into a portal vessel (*h.p.v.*) in the pars tuberalis: the subsequent fate of such a vessel is as follows. It passes upwards in the pars tuberalis and then enters the neural portion of the stalk and becomes ensheathed for a certain distance in a neuroglia sleeve where its course is tortuous, and finally it breaks up to take part in the formation of the secondary capillary network.

In the lower part of this vessel four round globules of colloid are shown in Plate I, fig. 1, lying in single file in the channel. Looked at under the microscope, these globules are homogeneous and refractile. A little lower at the site

marked *X* there is a sinusoid of the anterior lobe cut almost transversely, which contains three rounded globules of colloid, smaller than those in the hypophysio-portal vessel.

Plate I, fig. 2 is taken from a section in the same series as fig. 1; here another hypophysio-portal vessel (*h.p.v.*) happens to be cut for a long distance [*XX*] in the section as it is passing upwards. This also contains a number of colloid globules of various sizes lying within the lumen like a string of beads. In figs. 1 and 2 the hypophysio-portal vessels shown have not yet plunged into the neural portion of the stalk.

Text-fig. 3 is a microphotograph of a coronal section of the pituitary of a full-term foetus. This section is stained with haematoxylin and eosin. It

Text-fig. 3.

Text-fig. 4.

shows hypophysio-portal vessels in the process of leaving the pars tuberalis and entering the neural portion of the stalk [*XXX*].

Text-fig. 4 shows a frontal section through the stalk, both the neural portion and the pars tuberalis can be seen—and a number of the hypophysio-portal vessels are visible as they are passing, surrounded by glia sleeves (*g.s.*), towards the region of the secondary net. The site of the secondary net (*s.n.*) beneath the ependymal floor of the infundibular recess of the 3rd ventricle can also be seen.

Plate I, fig. 5 is a high-power view of the region of the glia sleeves.

Plate I, fig. 6 is a high-power view of the region of the secondary net.

Text-fig. 7 shows a frontal section of a pituitary attached by its stalk to

the hypothalamic region: the optic tracts (*O.T.*) are seen laterally. Into the anterior lobe of this gland a puncture injection of Indian ink was made prior to fixation and the site of the puncture (I) corresponded to the place of the large sinusoid containing colloid globules shown in Plate I, fig. 1. From this spot the ink entered some of the portal vessels and can be seen plainly in them. It also penetrated to some extent into the secondary net in the hypothalamic region.

In this figure the position of the nucleus paraventricularis (*n.p.*) and of the nucleus supraopticus (*n.s.op.*) can be seen.

Text-fig. 7.

The ink, besides being present in the secondary net beneath the floor of the ventricle, has been seen in minute vessels rising close under the ependyma of the lateral walls of the ventricle towards the site of the nucleus paraventricularis. The ink particles have not been seen actually among the cells of the nucleus.

Also passing laterally from the secondary net beneath the floor of the infundibular recess, small particles of ink have been encountered. They have not been found amongst the cells of the nucleus supraopticus, but their position seems to us to indicate the possibility that the secondary net sends prolonga-

tions in this direction as well as dorsally in the direction of the nucleus paraventricularis. These nuclei, supraopticus and paraventricularis, have a good systemic arterial supply.

In studying the very voluminous literature on the minute structure of the pituitary we have found statements which indicate that many observers have seen the hypophysio-portal vessels of our account, but without (excepting Pietsch) attaching to them the significance which we have given.

Looking for an excretory path from the hypophysis, Lothringer observed in the "Umschlagteil" of the hypophysis (the place where the anterior lobe is continuous with the pars intermedia on the ventral aspect of the stalk, at its lower end) a peculiar intermingling of epithelial cells with large vessels and supposed that this might be the resorption place of the gland ((1), pp. 264 and 290).

Edinger had different ideas on the pathways of hypophysial excretion. He found that Indian ink puncture injections, forced into the tissue of the anterior lobe, resulted in the appearance of long strands of ink extending from the hypophysis to the hypothalamic region, *along the vessels*. This implies that the vessels were present in his preparations, but he was looking for perivascular spaces and so did not appreciate the significance of the vessels ((2), p. 502).

Herring seems also to have observed these vessels. He says ((3), p. 155): "Some of the veins from the anterior lobe appear to take a similar course, passing through the epithelial investment of the neck of the infundibulum to run into the nervous portion; ....."

Trautmann has also observed that at the "Umschlagteil" the pituitary has a distinctive appearance when seen under the microscope, being characterised by an unusual richness of vessels ("Reichtum an Gefässen") ((4), p. 341). He also noted that the tissue surrounding the stalk is greater in amount ventrally and laterally than it is dorsally, and that it ends in the nervous substance at different levels towards the tuber cinereum, varying according to age, species, etc. ((4), p. 341).

Berkeley says ((5), p. 517): "The anterior or glandular portion is attached loosely to the rounded base of the infundibulum by connective tissue, and a large number of vessels, both veins and arteries, that directly pass into it from the substance of the infundibulum and to the 'lobus infundibuli'"; but he did not consider these veins as being any other than ordinary systemic vessels.

Collin says ((6), p. 41): "Aussi, les vaisseaux de la pars tuberalis accompagnés de leur trame conjonctive sont-ils, en même temps, les vaisseaux de l'infundibulum, où ils pénètrent avec une partie de cette trame conjonctive."

De Beer ((7), p. 98) speaks of the probability that products of the pituitary (other than those of the anterior lobe proper) may be blood borne.

Dostoiewsky's attention was also attracted by large vessels rising from the central part of the glandular lobe and taking a course dorsally towards the stalk ((8), p. 596).

Tello ((9), p. 156) gives a clear description of the distal part of our

hypophysio-portal vessels. He saw them at the lower end of the stalk going on the surface of it and having a tortuous course after they penetrate into the stalk, and he says that they branch and become more complicated as they approach the infundibulum. He says: "Los vasos de este trozo del tallo pituitario...caminan de preferencia por la periferia, siguiendo ensortijadas tragectorias y en manojos, pero emiten numerosas ramas que penetreten en el espesor del tallo....Estos pelotones son tanta más frecuentes y complicados cuanto más nos acercamos al infundibulo."

Unfortunately Tello worked with material which did not include a portion of the brain attached to the hypophysis and so he could not follow the entire course of these vessels and see their relation to a secondary net in the hypothalamic region. So Tello concluded that these vessels passed from above, down to the hypophysis and also (because of a resemblance of these vessels to some vessels of the cerebral cortex in atrophia senilis) came to regard them as being of a pathological nature.

It will be clear, from this short review, that the literature contains many references to the vessels which we have named hypophysio-portal, but so far as we have ascertained no one suspected that they were placed between two nets of distribution, i.e. the sinusoids of the buccal hypophysis and the capillaries of the neural hypophysis on the one hand and the secondary net in the hypothalamus on the other.

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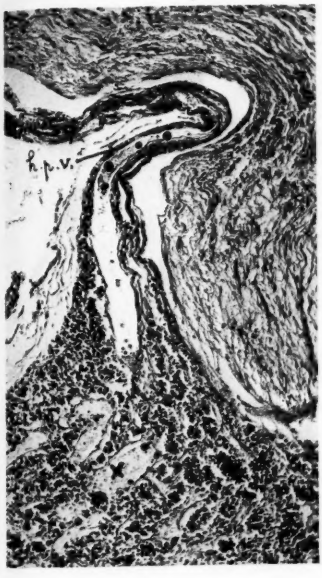

Fig. 1.

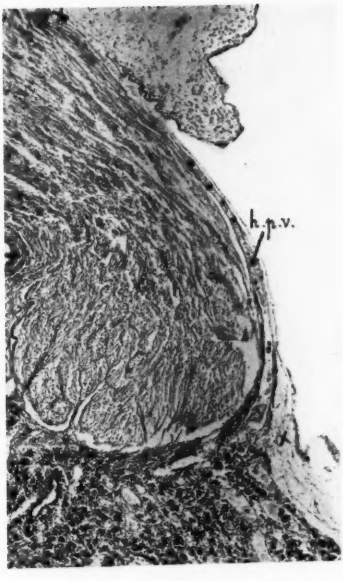

Fig. 2.

Fig. 5.

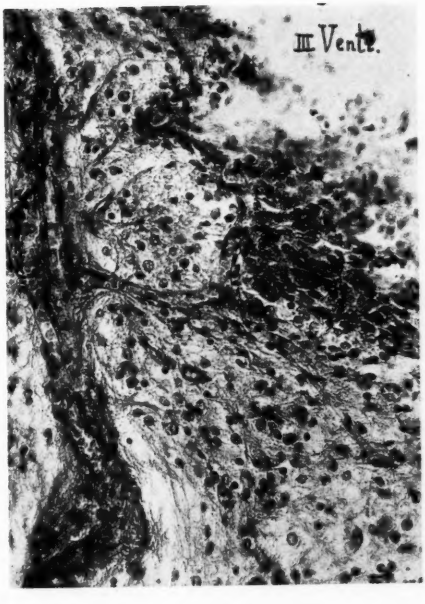

Fig. 6.

THE AFFERENT NERVE SUPPLY OF THE MESENTERY AND ITS SIGNIFICANCE IN THE CAUSATION OF ABDOMINAL PAIN

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INTRODUCTION

THE sensitivity of the mesentery to ordinary mechanical stimuli and its possible rôle in the causation of abdominal pain, has recently been brought to the fore largely through the writings of Tyrrell-Gray. He described (1922) the mesentery as exceedingly sensitive to every kind of stimulus, mechanical, chemical and thermal, and advanced the view that true visceral pain primarily arises from the mesentery, partly by impulses arising in the Pacinian corpuscles. In other papers (1926 and 1930) he suggested that the Pacinian bodies, together with the reflexes they initiate, are to be regarded as the normal means of protection of the mesentery against mechanical tension in the erect posture. Their stimulation excites reflex immobility of the abdominal wall, i.e. a protective mechanism termed the musculo-mesenteric reflex.

On the basis of the results of animal experimentation Breslauer (1921) suggested that the impulses which initiate visceral pain do not arise in the intestine but in the mesentery, and in particular in the mesenteric blood vessels. He was able to elicit pain reactions in his experimental animals by traction on the mesentery but not by distension or stretching of parts of the intestine which had been isolated from their mesenteric attachment. He also observed that areas of the peritoneum which contain large blood vessels are more sensitive than areas in which no large vessels are present. This latter observation had previously been made by Wilms (1904), who accounts for the pain of intestinal colic as being the result of stretching of the mesentery proximal to the stricture; thus a loop of bowel contracting on its contents at the proximal side of a constriction endeavours to assume a straight form, but is prevented by the limited extent of the mesentery. This results in stretching of the mesentery and so causes pain.

In reviewing the literature it appears that the sensitivity of the mesentery to ordinary mechanical stimuli has been open to some doubt by the several investigators. It was the original researches of Lennander (1903 and 1906 *a* and *b*) which first called attention to the fact that there is a distinct contrast in the sensibility of the parietal and the visceral peritoneum. From his careful and systematic observations under local anaesthesia, Lennander established that the parietal peritoneum is intensely sensitive to pain, though not to pressure, heat or cold, and that the abdominal viscera including the mesenteries and great omentum,

are insensitive to the ordinary painful stimuli such as pressure, cutting and stretching. From the work of Ramström (1905 and 1908) it was known that the parietal peritoneum is richly supplied with afferent fibres from the cerebro-spinal nerves, and Lennander concluded from his observations, that all tissues which are innervated solely by the vagus and sympathetic (such as the visceral peritoneum and the abdominal organs) are *insensitive* to pain.

Lennander's findings in regard to the mesentery are vague. Drag on the mesentery always produced dull nauseating pain, vaguely localised to the middle of the abdomen, and often associated with vomiting. He describes operations in which the mesentery is subjected to firm compression between the fingers, and stretching without any drag on its root, and no pain was evoked, but later he speaks of a case in which gripping the mesentery of the appendix with forceps caused severe pain, indeed the most severe of all, when all drag upon the part was avoided. He also records the result of an experiment with a piece of ileum clamped off; when inflated with air, the bowel straightened, the mesentery became stiff and assumed a fan-shaped form, and the patient complained of pain. This passed off as soon as the bowel was emptied of air, and the mesentery allowed to return to normal. This sensitivity of the mesentery to stretching he considered was probably due to pulling on its parietal attachments at its root. Despite his somewhat inconclusive findings Lennander considered the mesentery, along with the visceral peritoneum, as devoid of sensation, and from his observations on the sensitivity of the abdominal cavity, he advanced the theory that no pain originated directly in the viscera, and that all visceral pain was the result of inflammation or traction on the parietal peritoneum and its subserous connective tissue.

Mackenzie (1920) confirmed most of Lennander's observations, and from the cases quoted he appears also to have regarded the mesentery as incapable of responding to ordinary mechanical stimuli. Mackenzie considered the parietal peritoneum really as insensitive as the visceral peritoneum, its apparent sensibility being due to the extremely sensitive subserous connective tissue immediately adjacent. He explained this on the basis of different innervation, considering the serous layer as possessing purely sympathetic innervation, whilst the subserous layer is richly supplied with fibres from cerebro-spinal nerves. But this distinction between an insensitive serous membrane and a sensitive layer immediately external to it, is difficult to believe, and moreover, there does not appear to be any histological evidence in support of it. Although the theories of Lennander and Mackenzie on the causation of visceral pain are not in accordance, yet the general facts elucidated by them concerning the sensitivity of the various abdominal contents have been confirmed by other investigators, and are now generally accepted, except in the one particular instance of the mesentery.

Many other surgeons working under local anaesthesia found the mesentery and mesocolon extremely sensitive to ordinary mechanical stimuli. Kappis (1925) laid great stress on the sensitivity not only of the parietal peritoneum,

but of the mesenteries, and showed that the gastro-hepatic omentum, mesentery and mesocolon are highly sensitive to mechanical stimuli. Finsterer (1926) also disagrees with the view that manipulation of the mesentery, apart from traction on its root, is painless: and he emphasises the fact that mesenteric anaesthesia is required in cases of resection for a movable ulcer or cancer under local anaesthesia, and proves entirely satisfactory where all dragging on its root can be avoided. When this is impossible, the peritoneum of the posterior abdominal wall must be anaesthetised. Mayo (1929) holds the opinion that stretching of the visceral tissues can provoke pain, and he says that, with the abdomen open, splanchnic anaesthesia frees the whole abdomen of pain, *yet* local anaesthesia in the abdomen is secured by injecting local mesenteric areas, a procedure often advantageous over general anaesthesia. Mitchell (1911) writes that with "local anaesthesia it is very evident that only those procedures are painful which involve the parietal peritoneum or *mesenteries*," and Hirschel (1914) speaks of the pain caused by squeezing and pinching the mesentery, which renders simple ligature of this tissue so painful.

Morley (1931) in recent years has established and in many ways revised the known facts regarding abdominal sensitivity. His researches under local anaesthesia for abdominal section have confirmed, amongst other observations, the acute sensitivity of the parietal peritoneum and the insensitivity of the visceral peritoneum and *great omentum* to the ordinary methods of mechanical stimulation. He records (pp. 71 and 136) several cases in which, under local anaesthesia, the mesocolon and mesentery, when gripped with two pairs of dissecting forceps to within an inch or so of the attachment of the bowel, and torn, caused distinct pain. As a result of these observations, Morley concluded that though the intestine, both small and large, is completely insensitive, the mesentery is decidedly sensitive from its root to a point a little distance away from its attachment to the bowel. The explanation offered by Morley is that the posterior parietal peritoneum with the mesocolon and mesentery of the small intestine, up to a point an inch or so from their attachment to the bowel, are all supplied by cerebro-spinal sensory nerves. And he goes on to say in relation to the presence of Vater-Pacinian corpuscles in the mesentery: "Although further research is needed on the distribution and function of these corpuscles in the mesentery, there is good reason to believe that they are end organs of sensory cerebro-spinal nerves, and they are possibly concerned with pressure pain. Since they occur only on sensory somatic nerves they must be derived from the somatopleure. The division between the splanchnopleure and somatopleure of the embryo is usually assumed to be situated at the root of the mesentery. But the sensitivity of the mesentery and the distribution of Pacinian corpuscles in the mesentery suggest that the true separation between these two layers, so profoundly different in function as regards their means of defence against injury and disease, is really much nearer to the attachment of the mesentery to the bowel than has hitherto been supposed."

It is thus with a hope that some contribution could be made towards the

understanding of some of the more puzzling aspects of abdominal pain, that an attempt has been made here to consider how far some of the clinical findings and conclusions are in accordance with anatomical and histological facts. A complete investigation of the occurrence of Pacinian corpuscles in the mesentery, both in Man and in the cat, has been undertaken, and experimental and histological methods have been adopted to prove if possible the source of origin of the issuing nerves. An account is given of the nerves supplying the mesentery, and a description of the types of nerve endings found throughout its substance. An explanation, founded on histological fact, is offered for the acute sensitivity of the mesentery, and observations are presented which seem to offer some direct experimental support of Morley's theory of the true junction between splanchnopleure and somatopleure.

THE GROSS ANATOMY OF THE NERVES OF THE MESENTERY

In the strictly anatomical sense, Robinson (1899) points out that the mesentery is composed of (*a*) a central mesodermic structure, consisting of connective tissue, nerves, blood and lymph vessels, and (*b*) a thin peritoneal covering on each side consisting of endothelial cells. Robinson is very insistent that these three layers should be recognised, for, he says, "No advance in the knowledge of the mesentery can be expected while the old view is retained, which considers a mesentery as a duplicature of the peritoneum." And he goes on to show how, even in the first month of embryonic life, these layers are differentiated and can be recognised. This recognition of the mesodermic core, and of the fact that the mesentery is a separate entity and not merely a highway for blood vessels and nerves destined for the supply of the intestines, will help us to understand the significance of the afferent innervation to this structure, to be described shortly.

It is clearly evident there are two known sources of nerve supply to the mesentery, sympathetic through the splanchnics, and parasympathetic from the vagi. The branches of the lumbar sympathetic ganglia are uncertain in their number and distribution. The majority, apart from the well-known grey rami to the spinal nerves, pass to the aortic and hypogastric plexuses, and no branches are described so high up as the superior mesenteric plexus.

In the cat Ranson and Billingsley (1918) have shown that the splanchnic fibres leave the sympathetic trunk in a series of six to ten small nerves. The first of this series is much the largest and corresponds to the greater splanchnic nerve in Man. The level of the trunk at which this nerve is given off varies, but is usually about the thirteenth thoracic ganglia. Since it is well known, as they point out, that fibres of the splanchnic nerve come from segments as high as the fifth and sixth thoracic, it is obvious that these fibres must have descended in the sympathetic trunk to the point of origin of the splanchnic nerve. According to Ranson and Billingsley, other splanchnic fibres are given off in the cat, somewhat irregularly from the upper five lumbar ganglia and internodal

segments, but no mention is made of their distribution and ultimate destination.

A series of dissections, with the aid of the dissecting microscope, of the lumbar sympathetic trunk has revealed an occasional supply to the coeliac plexus from the upper lumbar ganglia, particularly of the left side. This arrangement was found in both the human and animal material, and had an important bearing on the experimental work, to be described shortly.

From a functional aspect, the nerves in the mesentery can be considered as:

(*a*) Nerve fibres destined for the supply of the intestinal wall and merely running through the mesentery, i.e. *Intestinal Nerves.*

(*b*) Nerve fibres for the innervation of blood vessels in the mesentery, i.e. *Vascular Nerves.*

(*c*) Nerve fibres ending in the mesentery itself, i.e. *True Mesentery Nerves.*

The first and probably also the second group are for obvious reasons both efferent and afferent: the latter group, however, is presumably only afferent, as there are, as far as we know, no free muscle fibres in the mesenteric tissue proper. Although necessarily these three functional groups merge into one another when considered in the light of gross anatomy: only the latter group, upon which presumably the sensitivity of the mesentery depends, is dealt with in this work. The possibility of the vascular nerves conveying sensory impulses cannot be excluded, but it was found necessary to limit the field of investigation considerably, to allow for more careful study, and in view of the many problems that presented themselves during the course of this work.

THE TOPOGRAPHY OF THE PACINIAN CORPUSCLES IN THE MESENTERY

The presence of these bodies around the head of the pancreas, especially in the cat, has for long been well known, and Ramström (1905) has described them in varying numbers in the anterior parietal peritoneum. Lawrentjew (1925) and Dowgjallo (1925) have made similar studies in the mesentery and mesorectum of the cat respectively, but there is little or no evidence of the exact distribution or proportion of these bodies in the human mesentery. On account of the overwhelming preponderance of the corpuscles in the cat, it was decided to make an initial study of them in this animal. For this twenty animals were examined, all of normal health and average weight of $1\frac{1}{2}$–2 kg. No staining was found necessary in this part of the work, the Pacinian corpuscles standing out as small semi-translucent oval bodies about 1 mm. in size (Plate I, fig. 1).

The animals varied greatly in their relative number of corpuscles, some demonstrating as many as 150 in the mesentery, others showing only five or six. The average number found was about fifty. The corpuscles were present usually in large numbers in the mesentery and mesocolon, where they were usually seen by the naked eye. In no case were any corpuscles found in the

great omentum, but the greater amount of fat here obscured the vision in many cases. The pancreas, especially after fixing, dehydration and clearing by the *Spaltiholz* method, was frequently packed with corpuscles, as many as fifty in some cases being seen embedded in the substance of the gland. Paraffin sections of the pancreas, and mesenteric lymph glands showed that the Pacinian corpuscles in all cases lay in the capsule and interstitial tissue, and never in the true glandular tissue itself. They were commoner in the mesentery than in the mesocolon: the total number in each usually bearing a relation of about 3 to 1 respectively. They were much commoner in the neighbourhood of the *base* of the mesentery, though they did reach close up to the border of the attachment of the gut. They were much commoner in the upper part of the mesentery than in the lower part. They usually lay along the course of the blood vessels, but occasional corpuscles were seen lying apart in the less vascular parts. The long axis of the corpuscle usually lay in the same direction as the line of mesenteric vessels and nerves. They often lay in groups of two or three, or occasionally more, packed closely together; whilst the next few inches of mesentery might contain an isolated corpuscle or even none at all. Occasionally a great number occurred in a bunch together. In one case it was possible to count fifteen lying close together near a lymph gland. The afferent nerve entering the corpuscle appeared to be myelinated and was traced in some cases, by the aid of the dissecting microscope, back to its emergence from the coeliac ganglion and superior mesenteric plexus.

A second investigation was then made of a similar nature in the human subject. As the post-mortem specimens were so difficult to obtain entire, foetal tissues were used instead. Ten still-born foetuses were examined in a precisely similar manner to the method described above. The Pacinian corpuscles were *very* difficult to find by naked eye, owing to the greater amount of fat present than in the cat. Serial sections were made of the entire human (foetal) mesentery in three cases. In one case, no corpuscles could be found in any of the sections. In the others, the corpuscles were seen chiefly in the proximal $\frac{1}{2}$–1 in. of the mesentery, i.e. close to the base. They were not nearly so numerous as in the cat. They frequently lay in pairs and were seen in some cases lying embedded, as in the cat, in the interstitial tissues of the pancreas and mesenteric lymphatic glands. Plate I, fig. 2 shows a section (stained by haemalum and eosin) of two Pacinian corpuscles lying in the middle zone of the foetal mesentery, half-way between its root and the attachment of the gut. The occurrence of these bodies in the mesentery of Man, close to the attachment of the gut, as seen so clearly in the cat, was not observed, though it is mentioned by Kölliker (1860) in his *Manual of Microscopic Anatomy*.

THE NERVE ENDINGS OF THE MESENTERY

The presence of Pacinian corpuscles in the mesentery has been known for many years. First noticed by Vater and later re-investigated by Pacini, they have been the object of interest to many workers including Henle, Kölliker, Merkel and Krause. Their peculiar frequency in the mesentery of the cat, a fact well known to all histologists, is as yet unexplained. Other types of nerve termination in the mesentery, apart from those in the walls of blood vessels, have been described by two observers. Robinson (1897), using the gold chloride method of staining, mentions the presence of thread-like endings "like a long drawn out dagger" from non-medullated nerves, and also of a fine plexus of non-medullated fibres. He does not go into any detailed description: nor is there any account given of their arrangement or distribution in the substance of the mesentery. Kadanoff (1924) published a short account of his study of the nerves of the mesentery, using the sodium-silver method of Stöhr. He was successful in establishing the presence of very fine medullated nerves which, after a fairly long course, divided dichotomously and ended free in the connective tissue. He considered their form and manner of ending was suggestive of an explanation for the diffuse pain sensibility of the mesentery, and he suggested that the type of stimulus required is in all probability a considerable degree of extension of the mesentery. In one case, in a human mesentery, he observed a nerve fibre which, after a fairly long course, ended freely in a varicose state surrounded by a thin connective tissue covering. Kadanoff also described in greater detail the fine plexus of non-myelinated fibres, mentioned by Robinson. He considered the network was sealed, having no actual nerve termination, and could be looked upon as "association bundles." Dogiel (1902) and Timofejew (1902) have described similar nerve endings in the parietal peritoneum lining the anterior abdominal wall and the under surface of the diaphragm.

For this part of the investigation many animals were used, and careful systematic examinations under the microscope were made of the entire mesentery in each case, after staining with intra-vitam methylene blue by injection. A saline solution of 1 in 2000 was used, and a satisfactory technique was finally acquired which would give a uniformly stained picture in practically all cases. This method was used throughout this investigation. Owing to the nature of the method, the study was necessarily confined to animals, and the cat was chosen, for reasons stated above, as the most suitable. The human material was only obtainable so long after death as to be useless for the methylene-blue method.

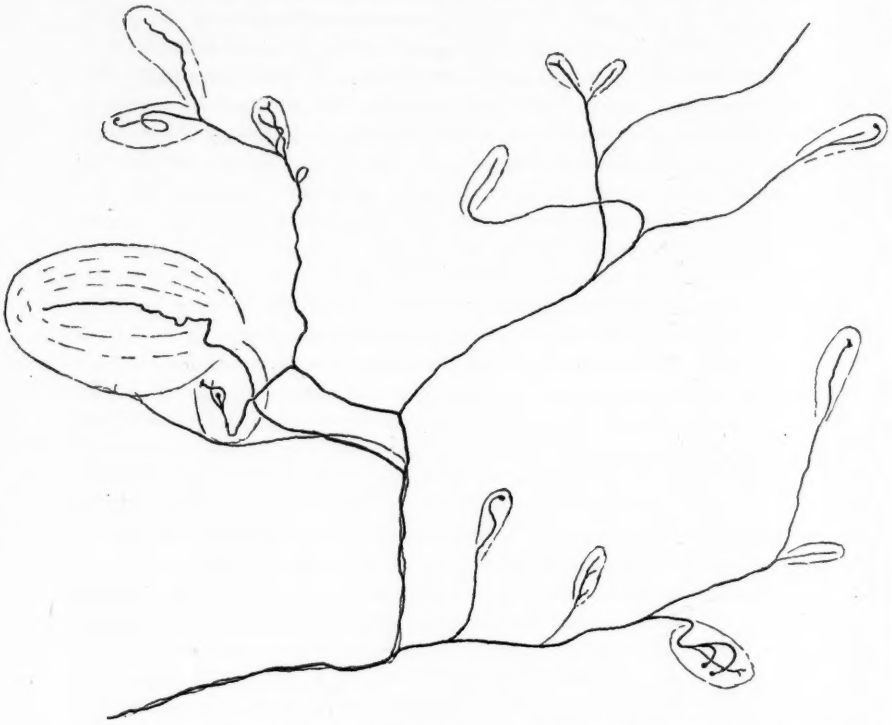
Three main types of nerve endings were revealed in the mesentery and could be clearly and distinctly recognised.

(1) *The encapsulated type*, in histological appearance the typical Vater-Pacinian corpuscles. It was found, however, to vary considerably both in size and shape. So much was this the case that it seems better to use the wide

term of "end-bulb" rather than designate all under the more specialised type of "Pacinian body." Some were so large as $1 \times 0{\cdot}6$ mm., whilst others measured only $8 \times 4\mu$. Two types of corpuscles could be clearly recognised from their size, although all intermediate forms existed (text-fig. 1):

(*a*) A large type, measuring from $\frac{1}{2}$ to 1 mm. in length, and usually situated at the termination of a myelinated nerve.

(*b*) A small type, of about 1/100 mm. long, found invariably on short lateral offshoots from the main axon.



Text-fig. 1. Diagram to show termination of a myelinated nerve in the cat's mesentery. Intra-vitam methylene-blue preparation. Note the two distinct sizes of the end-bulbs.

The nerve termination in the latter appeared as a short varicose stalk and at first appeared as free nerve endings, but on careful focussing they were seen to be surrounded by a thin connective tissue covering. It is very questionable whether these were true Pacinian corpuscles, as they did not show all the typical features of such bodies. They were, however, from their appearance end-organs of an encapsulated type, and seemed to correspond to the example found in the human mesentery by Kadanoff. In shape most were ovoid, but

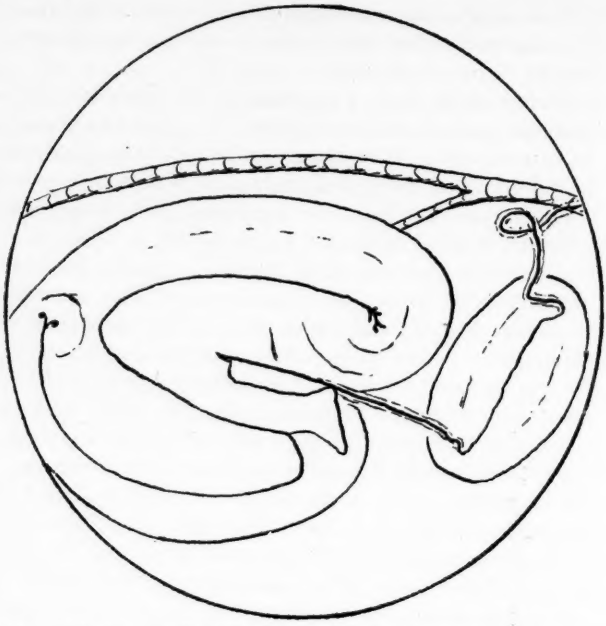
completely circular corpuscles were often seen. A peculiar and not at all uncommon type, was one in which the corpuscle was bent upon itself in the form of an inverted U.

The constitution of the larger encapsulated end-organs was the same, the typical laminated capsule with a central core through which the main afferent nerve ran to its termination. The main nerve fibre of the corpuscle can be seen to be definitely myelinated, the typical appearance of Ranvier's nodes standing out clearly in most cases. The latter area was usually more deeply stained than the rest of the nerve axon, and could be recognised at once under the low power. After a distance, corresponding to about a quarter the length of the corpuscle, the nerve fibre can be seen to lose its medullation and can be traced through the central core of the Pacinian body to the opposite pole where it usually terminated in two or more bulbous extremities. Its course through the corpuscle was not usually straight: it frequently formed several loops in the proximal pole before it entered the central core, and at the distal end it was very often curved in its course, forming a half circle. This wavy course of the nerve fibre is not emphasised in most descriptions of these end-organs.

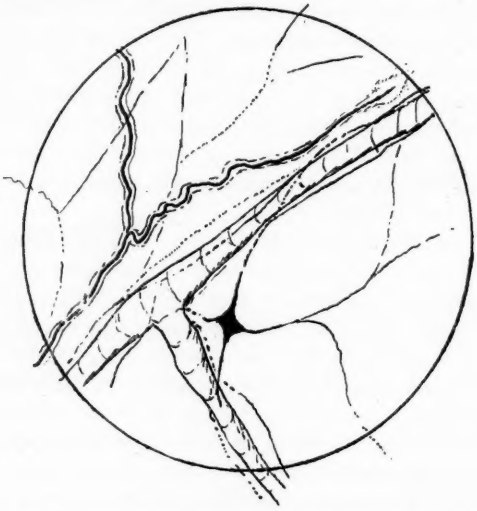
From the nerve fibre, whilst embedded in the corpuscle, short lateral offshoots could apparently be seen in some cases, but on careful focussing these appeared to be entirely separate from the nerve fibre. True branching of the nerve axon inside the corpuscle is, however, not at all infrequent. The nerve fibre could be seen in some cases, as described by Van de Velde (1907), ending in an irregular bulbous termination, in which can be distinctly seen a dense network of neuro-fibrils, continuous with the longitudinal fibrils stained in the main axon. But not in all cases does the nerve fibre end inside the corpuscle. In four cases the nerve ran its entire course through the corpuscle and emerged at the opposite pole, without any nerve termination (text-fig. 2). One nerve fibre can divide up and supply two corpuscles, and this arrangement of two or more Pacinian bodies being linked together on one common nerve fibre, appears to be important in view of the possible function of these bodies. The unmyelinated nerve fibres which are distributed to the outer aspect of their capsule were also clearly recognisable.

These encapsulated end-organs lie in every case embedded in the substance of the mesentery, deep to the endothelial covering. They can be isolated from the surrounding fat and picked up by means of fine forceps, with the aid of the dissecting microscope. Pacinian bodies of exactly similar type were also found in the parietal peritoneum on both the anterior and posterior abdominal wall, in the peritoneum covering the superior surface of the bladder, and in the transverse mesocolon.

(2) *Free nerve endings.* Running into the mesentery were other myelinated nerve fibres which travelled in some cases almost to the attachment of the gut. The calibre of these nerves was quite as large as those terminating in Pacinian bodies. No *particular* dichotomous division could be seen in any of the preparations: all the myelinated nerve bundles and fibres, which usually run



Text-fig. 2. Diagram to show myelinated nerve passing through one corpuscle to terminate in an adjacent complex end-bulb. Intra-vitam methylene-blue preparation.



Text-fig. 3. Diagram to show unmyelinated nerve network with ganglion cell, and a "free" nerve ending of an adjacent myelinated nerve. Intra-vitam methylene-blue preparation.

with the blood vessels, divide in this manner at each bifurcation of the accompanying artery and vein. Some of these myelinated nerves were seen to end in long tail-like processes in the substance of the mesentery (text-fig. 3). The myelinated sheath seems to have disappeared at the final termination, and the axon is slightly swollen along its course. They are not present in any great number and were very difficult to find, as they frequently lie near to the blood vessels. No arborising terminals could be seen in any of the mesenteries examined. Similar free nerve endings were found in the transverse mesocolon and in the peritoneum covering the superior aspect of the bladder.

(3) *A fine nervous plexus* could be traced through the entire mesentery in the best stained preparations (Plate I, fig. 4). It was non-medullated throughout and was definitely continuous with the fine plexus of unmyelinated nerves spun round the blood vessels and capillaries of the mesentery. It was found as well marked at the root as at the peripheral border of the mesentery. It extended out into the very thin avascular portions of the mesentery, which are composed almost entirely of the two endothelial layers of peritoneum. It has been traced on to the visceral peritoneum covering the intestines and bladder, and also into the substance of the liver and kidney.

It possessed at wide intervals small nerve ganglion cells, the processes of which pass outwards and take part in the formation of the fine network. The fibres often showed small fusiform swellings, which with high power appear cellular in structure, no doubt the nuclei of the neurilemmal sheath. Robinson holds the view that there is contact without continuity, that "the meshwork of nerves is produced by the nerve fibres coursing alongside each other, yet preserving their exact identity." From the preparations examined in this work, the single fibres appeared to branch and anastomose in a true network arrangement. Fine twigs could be seen occasionally issuing from this plexus and apparently ending freely amongst the endothelial cells. It therefore appears to be not a closed system. It is possible that this feature may be due to the dye having not penetrated sufficiently far along these fine nerve branches, but the repeated finding of this arrangement was very convincing.

The presence of this plexus in so many of the preparations examined is convincing. There can be no question of white or elastic fibres or fine capillary twigs similating a plexiform arrangement: the identification of the small ganglion cells and the connection with the fine unmyelinated nerves around the blood vessels, is conclusive evidence of its nervous origin.

EXPERIMENTAL DEGENERATION OF THE SPLANCHNIC AND VAGI

It is generally held by most observers that the main afferent nerve to the corpuscles in the mesentery is splanchnic in origin. Edgeworth (1892) by a series of sections made at right angles to the long axis of the Pacinian corpuscles, found that the nerve fibre was of the large medullated type as seen in

the splanchnics, i.e. 6·3μ in diameter on an average. The medullated fibres found in the vagal trunks were all smaller than this. Langley and Anderson (1894) from similar histological sections came to a similar conclusion. They found that in the cat, "the large sympathetic fibres (medullated) run chiefly, and perhaps entirely to the Pacinian bodies in the mesentery." There does not appear, however, to be any definite proof of the origin of the nerve entering these bodies, and according to Morley (cited above) the Pacinian corpuscles in the mesentery may be on cerebro-spinal fibres. This he inferred from the clinical observations under local anaesthesia. It is now well established that one cannot decide on histological appearances alone whether a nerve be sympathetic or somatic. Many sympathetic afferent fibres are known to be medullated, and recently Ranson and Davenport (1931) have shown that non-myelinated fibres may exist in the sensory somatic nerves.

From the account already given it is clear that the mesentery in itself, apart from the nerves running through it to supply the intestinal and vascular walls, possesses three possible sources of afferent innervation:

(1) Sympathetic—from the splanchnics, or possibly from the lumbar sympathetic cord.

(2) Parasympathetic—from the vagi.

(3) Somatic ? as suggested by the clinical observations.

It was therefore obvious that experiments would have to be devised whereby the sympathetic and parasympathetic innervation could be cut out independently or together: any residual afferent nerve endings must then necessarily be somatic. It was decided to cut both splanchnics in one series of animals, and both vagi as they issue through the diaphragm on each side of the lower end of the oesophagus in another series, and in a third series to cut both splanchnics and to remove the lumbar sympathetic chain on both sides. These results will be discussed later, but a brief description of the operative technique is given here for the sake of convenience.

Operative technique. Transperitoneal route

In all cases the animal was anaesthetised by ether and a mid-line abdominal incision made. In the series of splanchnic operations the splanchnic nerve was picked up on each side transperitoneally as it curves round the crus of the diaphragm. The guide to the splanchnic nerve was the suprarenal, but in most cases it was impossible to make a mistake as it could be seen shining through the posterior parietal peritoneum. The left splanchnic was always most difficult to reach, and the inferior vena cava had to be retracted to one side before the nerve could be divided. A quarter of an inch from the nerve was always excised to ensure complete division and to prevent any possibility of regeneration.

In the second series of operations, where the vagi were divided on both sides, this was performed by a collar incision around the oesophagus as it emerges through the diaphragm.

In all cases the operation was completed rapidly and the abdominal wall

resutured. The animal usually showed signs of recovery within half an hour after the operation, and its subsequent health was unimpaired. The animals were in all cases kept for at least 3–4 weeks to allow time for degeneration.

Series I. The first series of experiments carried out consisted of division of the splanchnic nerves on both sides of the body in the cat. The transperitoneal route as described was used in all cases. After a period of 3–4 weeks being allowed for degeneration of the distal portion of the nerve, the cats were stained by the methylene-blue technique as already worked out for the normal animals. Twenty animals were used for this part of the work: ten on which the operation of bilateral splanchnectomy had been performed, and ten normal cats which were used as controls and were stained with the same solutions and technique. In all cases the divided nerves were isolated and identified at post-mortem.

The results were as follows:

In the ten animals on which splanchnectomy had been performed, no nerve endings could be seen in the Pacinian corpuscles of the mesentery, except in one case, where a few corpuscles gave the normal appearance. Plate II, fig. 1 demonstrates the appearance of the corpuscles after bilateral splanchnectomy. In the series of ten controls, all showed the typical normal staining of the nerve ending in the Pacinian bodies, as previously described. Plate II, fig. 2 is taken from one of these cases and is placed in contrast to the empty appearance of the corpuscles after operation. The free myelinated nerve endings are difficult to find in the normal animal, but in two cases after splanchnectomy, examples of this method of termination were definitely seen and identified. The presence of the unmyelinated nerve plexus, after splanchnectomy, is to be expected in view of the presence of nerve ganglion cells in its connections in the mesentery.

A confirmatory series of similar experiments was carried out in three animals towards the end of this work, when the technique of staining was considerably improved and a positive result could be guaranteed in about nine out of ten cases. Exactly similar results were obtained, and again in this last series, one case occurred in which one or two corpuscles gave the normal appearance even after operation and both splanchnics had been cut. These lay all near the base of the mesentery. All the rest of the Pacinian corpuscles showed the "empty" non-stained appearance.

Series II. A second series of recovery experiments was then undertaken. For this five animals were used: the vagus on each side of the body was divided sub-diaphragmatically: and after the similar period of 4 weeks for degeneration to take place, the animals were anaesthetised and stained intravitally with methylene-blue. Five of the normal animals used in the first series of experiments were utilised again as controls, as the two series were worked out concurrently. The normal appearance of the Pacinian corpuscles was seen in every case (Plate II, fig. 3). No cases occurred in which the central nerve termination did not stain. The unmyelinated nerve plexus was present, and in one case the

appearance of free myelinated nerve endings was defined after both vagi had been cut.

Series III. In the commencement of this work some gross dissections of the nerves running in the mesentery of the cat had revealed a few nerve fibres which reached the coeliac and superior mesenteric plexuses from the first lumbar sympathetic ganglia. It was obvious that the possibility of these fibres taking part in the afferent innervation of the mesentery, must be first excluded, before one can safely presume any somatic supply. For this a third series of experiments was carried out on five animals. In all both splanchnics were divided as described above, and in addition the lumbar sympathetic cord was removed on both sides. The Pacinian bodies again showed no nerve endings stained, but the normal appearance of the nerve plexus was clearly seen. Only two free myelinated nerve endings were found in this series, but both were definitely stained.

Though a positive methylene-blue result can be accepted as conclusive evidence, a negative result is always open to the possible explanation that the dye has failed to outline the nerve terminals. The most convincing evidence that the negative results in the above series of experiments are due to true nerve degeneration, is the fact that only one of the ten animals, upon which bilateral splanchnectomy had been performed, showed any nerve ending in the Pacinian bodies: whilst all the controls, treated exactly in the same manner as regards staining, gave the typical appearance of the nerve terminations.

SUMMARY AND CONCLUSIONS

A description of the gross anatomy of the nerves of the mesentery in both Man and in the cat is given, and a connection between the first lumbar sympathetic ganglia and the coeliac plexus is described. An account is given of the exact distribution and proportion of the Pacinian corpuscles in the mesentery. The most striking feature is the great variation in the presence and numbers of these bodies both in Man and in the cat. They are embedded in the substance of the mesentery, deep to the true peritoneal lining, and are also found embedded in the interstitial tissue of the pancreas and mesenteric lymph glands. Their tendency to lie in groups is very striking. The main afferent nerve to the Pacinian body is myelinated, and in addition they receive small non-medullated twigs for the supply of the outer capsule. A satisfactory method of staining nerve endings has been acquired, and the different types of nerve terminations in the Pacinian corpuscles have been demonstrated. The occurrence of nerve fibres passing straight through one Pacinian body to end in one or more adjacent corpuscles has been confirmed.

The afferent nerve endings of the mesentery have been studied and reveal three types:

(1) Pacinian bodies.

(2) Free nerve endings of myelinated nerves.

(3) Free nerve endings of a fine plexus of non-myelinated fibres.

From experimental work, the afferent nerves of the Pacinian bodies in the mesentery have been shown conclusively to travel along the splanchnics. The function of these end-organs will be discussed in a subsequent paper.

The fine non-myelinated nerve plexus contains ganglion cells in the mesentery and appears to be purely sympathetic, both from its distribution throughout the visceral peritoneum and abdominal viscera and from experimental evidence. The function of this non-myelinated nerve plexus would appear to be similar to that of Auerbach's and Meissner's plexuses with which it is undoubtedly connected, namely the control of unstriated muscle and probably also for the transmission of the impulse which gives rise to the symptom of true visceral pain.

The free nerve endings of the myelinated nerves are rare. Although the results of experimental work are not sufficient to be conclusive, they appear to be neither vagal nor splanchnic, and they have been found after removal of the lumbar sympathetic chain. It is therefore legitimate to presume that they were probably somatic in origin, i.e. they pass up to the spinal ganglia via somatic nerves. Although the actual fibres could not be identified by gross dissection, there are many possible sources from the lower dorsal and lumbar spinal nerves. If we may thus correlate the anatomical and histological facts with the clinical findings, it would seem that it is these free nerve endings of myelinated nerves that give rise to the distinct pain experienced on cutting or tearing the mesentery. They are apparently not present in the visceral peritoneum covering the intestines, nor in the great omentum, which have been proved to be insensitive to ordinary mechanical stimuli. The variability in their number and distribution in the mesentery would account for the conflicting views held by surgeons on the sensitivity of this structure. This would appear to be the underlying anatomical explanation for the rather puzzling clinical findings on the sensitivity of the peritoneum. It provides further experimental evidence in support of the view, based on clinical investigations, that when pain is produced by mechanical stimulation, the stimulus affects tissues which are supplied by sensory cerebro-spinal nerve components not incorporated in the autonomic nerves.

These results therefore afford some evidence of the path by which afferent impulses from the mesentery reach the central nervous system: the balance of probability lies with the view that the mesentery possesses an afferent innervation from nerve fibres which travel via somatic nerves: and some evidence is brought forward in support of Morley's theory of the true junction of splanchnopleure and somatopleure lying much closer to the attachment of the gut to the mesentery than has been previously supposed.

To Mr Morley, Ch.M., F.R.C.S., I offer my sincere gratitude for suggesting and first interesting me in this problem. The work has been carried out in the Anatomy Department of the University of Manchester. It has been done entirely under the guidance of Prof. J. S. B. Stopford, for whose kind advice

and help and many encouragements I am deeply grateful. I wish also to thank Prof. Raper and Dr Schlapp of the Physiology Department for permission to use their laboratories, and Dr F. N. Marshall who acted as anaesthetist and was able to confirm each step in the nerve section experiments. Mr Gooding, of the Histological Department, has kindly done the microphotography for me.

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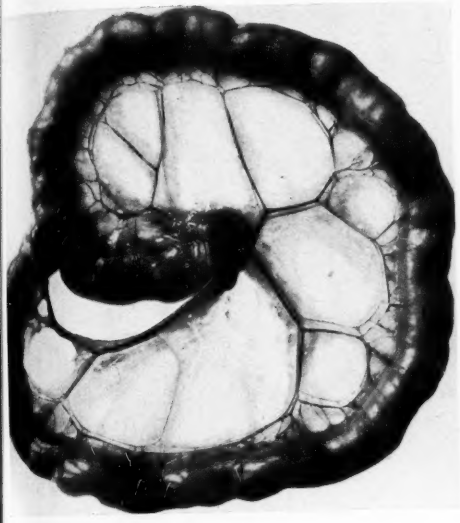

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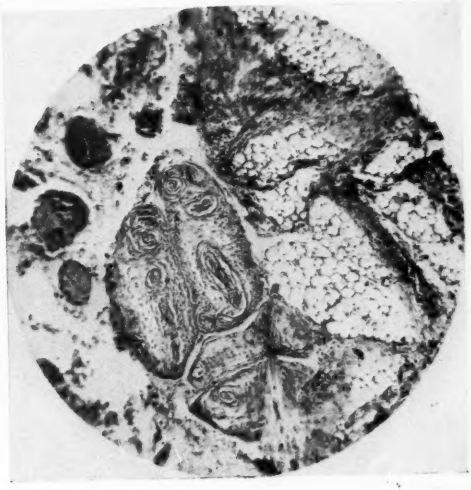
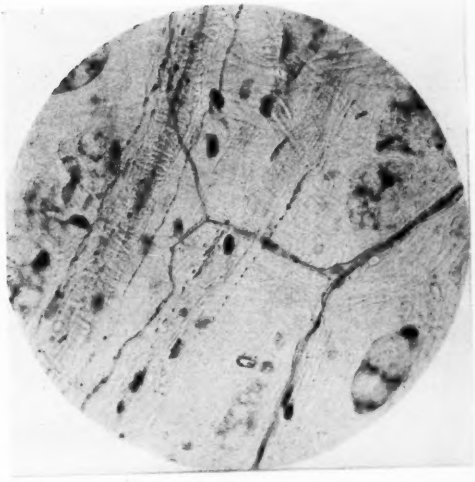


Fig. 2.

Fig. 3.



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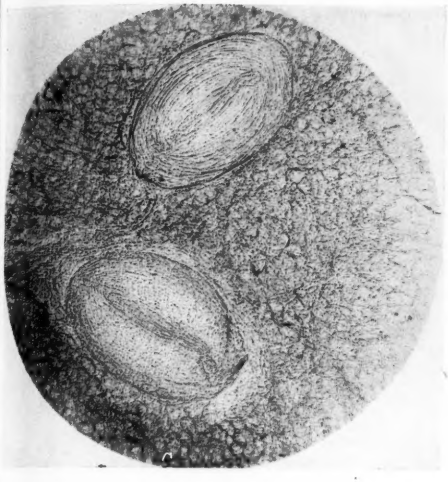

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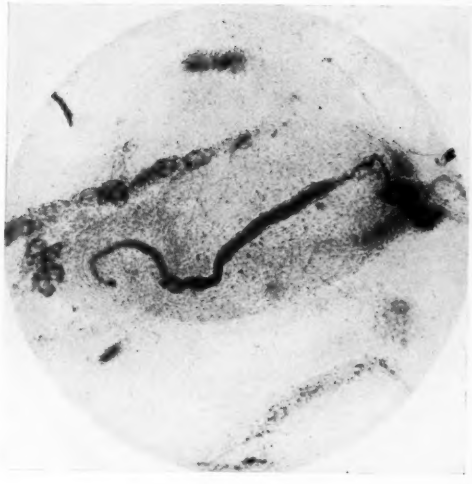

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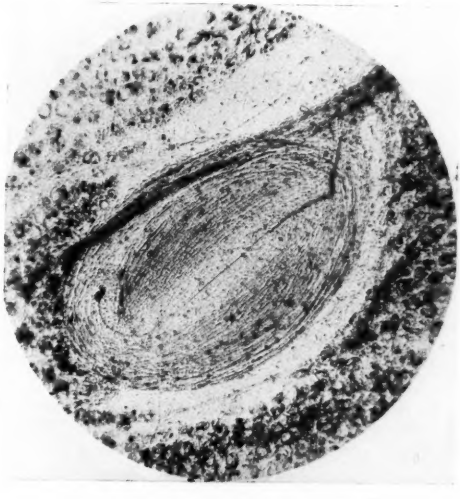

Fig. 3.

EXPLANATION OF PLATES

Plate I

Fig. 1. Photograph of portion of mesentery of cat, showing the appearance and position of the Vater-Pacinian corpuscles.

Fig. 2. Microphotograph of section of human mesentery (foetal), half-way between its root and the attachment of the gut. Stained haemalum and eosin. High power. Shows two corpuscles lying embedded in the mesenteric tissue.

Fig. 3. Microphotograph of section of cat's mesentery. Stained haemalum and eosin. High power. Shows similar appearance to Fig. 2.

Fig. 4. Microphotograph of mesentery of cat, showing nerve plexus connected with the fine unmyelinated network around the capillary. High power. Intra-vitam methylene-blue preparation.

Plate II

Fig. 1. Microphotograph of portion of cat's mesentery. High power. Intra-vitam methylene-blue preparation. Shows "empty" appearance of corpuscles following bilateral section of the splanchnic nerves.

Fig. 2. Microphotograph of Vater-Pacinian corpuscle in mesentery of cat, stained by the intra-vitam methylene-blue technique. High power. Shows typical normal appearance of nerve termination.

Fig. 3. Microphotograph of nerve termination in corpuscle, following bilateral section of the vagi. From mesentery of cat. Intra-vitam methylene-blue preparation. High power.

THE QUANTITATIVE STUDY OF LYMPHOCYTE PRODUCTION

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I. INTRODUCTION

Previous work on blood formation in fishes (1) led to a re-investigation of the known facts concerning the lymphoid tissues of Mammals, and their relation to the remainder of the haemopoietic system (2). As a result of this it became desirable to investigate the problem of lymphocyte production from a quantitative standpoint, and accordingly the present work was undertaken. It has been one of the more serious defects of haematological work in the past that it has been essentially qualitative in nature. The few observations which have been made (e.g. occasional counts of white and red cells in small quantities of blood or lymph) are insufficient for accurate quantitative study of the formed elements of the blood.

In this respect it is fortunate that the lymphocytes lend themselves to quantitative study more easily than any of the other formed elements of the blood. It is possible that some lymphocytes enter the blood directly as soon as they are formed, through the thin-walled veins found in lymphoid tissue and described in detail by Schultze (3); these lymphocytes cannot be measured. Large numbers of lymphocytes, however, first of all enter the lymph stream, and by it are finally conveyed to the blood. These can be counted with a fair degree of accuracy. It is possible, by tapping the thoracic duct immediately before it drains into the blood, to collect the major part of the body lymph and estimate its lymphocyte content.

It is rather surprising to find that in the past physiological investigation has been concentrated almost exclusively upon the study of the fluid content of lymph, without taking any note of its cellular constituents. Heidenhain, for example (4), in his classical paper on lymph formation, makes only a passing reference to the occurrence of lymphocytes in lymph. He had noticed that under certain conditions the lymph became somewhat turbid, and says (p. 228) in commenting upon this: "Unter dem Mikroskope sieht man oft, aber nicht immer, zahlreiche Leucocyten. Da das weissliche Aussehen auch dann beobachtet wird, wenn die Leucocyten sehr sparsam sind, konnen sie nicht die Ursache desselben sein."

Since Heidenhain's time numerous observers (Rous (5), Haynes and Field (6), and others) have made occasional counts of the lymphocytes both in

thoracic duct lymph and in lymph from other vessels. Only scattered observations have been made, however, with no attempt to analyse their total quantitative significance, or to correlate them with the lymphocytes of the blood.

II. MATERIAL AND TECHNIQUE

The present work was carried out on twelve dogs, ranging in weight frmo 9 to 14 kg. The animal, after 24 hours' starvation (during which, however, it was given abundant fluid in the form of water), was fed on half a pound of lard. Two hours later the dog was lightly anaesthetised with a C.E. mixture, and then through a cannula—to which was kept attached throughout the experiment a 50 c.c. burette—tied into the left femoral vein was introduced a solution of chloralose in normal saline, in quantites of 0·1 gm. of chloralose per kg. body weight. The anaesthetic effect of the chloralose would last about 5 hours, after which half the original dose would keep the animal comfortably anaesthetised for the remainder of the experimental period, though occasionally a third dose would be necessary. The experimental period usually lasted 9 hours.

The exposure of the thoracic duct may present a little difficulty. An incision about 4 in. long is made along the line of the left external jugular vein, extending down over the left pectoralis major muscle. The outer border of the left sterno-mastoid is defined, and by dissecting down in the interval between sterno-mastoid and external jugular vein one reaches the junction of the external and internal jugular veins, and a little below the further junction of the common jugular vein with the left subclavian vein. The thoracic duct is usually found on the inner side of this second junction, between the veins externally, and trachea and oesophagus internally. The direction of the duct is upwards and forwards until immediately before its opening into the vein, when it usually dilates into a small cistern and bends rather more sharply forwards.

This description is true of the average case, but it must be emphasised that from an anatomical point of view the termination of the duct is very irregular. Sometimes, immediately after the left cervical lymph duct has joined it, it divides into two or three small branches which open separately into the vein. There are usually one or more valves (often three or four in a row close to one another) in the duct near its opening into the vein, and these may be a source of trouble on introducing the cannula. The wall of the duct is exceedingly thin, and if the cannula cannot be coaxed past the valves the experiment often has to be abandoned. The least force tears both the valves and the vessel wall. Apart from the difficulty of introducing the cannula, the main complication to be feared is coagulation of the lymph. There is great variability in this respect. Sometimes the lymph shows no sign of clotting, at other times it keeps persistently clotting in the cannula so that the experiment may finally have to be given up. Anti-coagulants (e.g. leech extract, peptone) dare not be used, for, as pointed out by Heidenhain, they are powerful lymphagogues.

III. THORACIC DUCT LYMPH: AMOUNT FORMED AND CELL CONTENT

Amount of lymph formed

Drops of lymph from the cannula were collected in a graduated cylinder, which was emptied hourly and the quantity of lymph recorded. If the results are adjusted to a body weight of 10 kg., the average lymph flow per hour is 24 c.c. This corresponds fairly closely with the figure obtained by Heidenhain (25 c.c. per hour), and with those of other workers quoted by Heidenhain (*loc. cit.*). It is of interest to note that Heidenhain's figures were obtained with dogs which had been starved for 36–48 hours, whereas the dogs used in the present series were fed before the experiment. The quantity of lymph produced would appear therefore to be independent of the digestive processes. (For additional evidence to this effect see Heidenhain's paper.) Furthermore, in Heidenhain's experiments the entire experimental period did not last longer than 3 hours. In the present series the duration of the experimental period was usually 9 hours, during 7 of which lymph was collected.

Cell content of lymph

At the end of every hour, when the total lymph flow for that hour had been measured, three drops of lymph were taken from the cannula in a small paraffined tube, and used for a lymphocyte count. It was found that the count varied very little over a period of 1 hour, and in fact even over a period of several hours remains astonishingly constant (Table I). The lymphocyte count at the end of each hour represents with fair accuracy the lymphocyte count throughout the hour. If therefore at the end of 1 hour the lymph contained 10,000 lymphocytes per c.mm., and if the total lymph flow for that hour was 25 c.c., then the total lymphocyte output for that hour would be

$$25 \times 10{,}000 \times 1000 = 250{,}000{,}000.$$

Over a 24-hour period this would represent a lymphocyte output of 6,000,000,000. In exceptional cases (Table II), there may be a more marked difference between the hourly lymphocyte counts. In these cases the mean of the two counts was taken as the average count for that hour. As already pointed out, however, the difference between the hourly counts was not usually marked.

The total daily output of lymphocytes

Taking the average of the whole experimental series, we arrive at the following figures for the total daily lymphocyte production—worked out for a 10 kg. dog:

Lymph formed in 24 hours	= 576 c.c.
Lymphocytes per c.c. = 9040 (per c.mm.) × 1000	= 9,040,000
Total daily output of lymphocytes	= 5,207,000,000

These are average figures. The figures for each experimental animal may be worked out from a set of data of the kind given in Tables I and II.

Table I

22. iii. 32. Weight of animal 11,000 gm.

Time	Lymph collected c.c.	Lymphocyte count
1.25 p.m.	25	11,500
2.25 „	23	11,300
3.25 „	22	12,200
4.25 „	26	11,100
5.25 „	23	11,300
6.25 „	23	10,000
7.30 „	24	10,100

Lymph collected over 7-hour period	=166 c.c.
Percentage of fat in total lymph	=1·05 per cent.
Grammes of fat carried by lymph	=1·7
Total blood lymphocytes at 1.25 p.m.	=1,210,000,000
Total blood lymphocytes at 7.35 p.m.	=518,000,000
Lymphocytes collected from thoracic duct*	=1,549,200,000
Difference between blood lymphocytes at beginning and end of experimental period	=692,000,000

* Beginning from 1.25, when first blood count taken.

Details of anaesthetic

Chloralose gm.	Saline c.c.	Time
1·1	100	11.30 a.m.
0·5	50	3.0 p.m.
0·5	50	4.30 „
0·5	50	6.40 „

Table II

26. iv. 32. Weight 12,500 gm.
Blood volume = 962 c.c.

Time	Lymph (c.c.)	Lymphocytes	Hour average
3.12 p.m.	23	33,400	—
4.12 „	23	14,200	23,800
5.12 „	23	13,500	13,850
6.12 „	22	12,100	12,800
*7.12 „	29	10,100	11,100

* At 6.10 eight minims of 1 : 1000 adrenalin were given intravenously. There was a slight increase in lymph flow for the following 50 min., followed by marked diminution and increased coagulability of the lymph, so that the experiment had to be abandoned.

Total blood lymphocytes A†	=4,069,000,000
Total blood lymphocytes B	=1,608,000,000
Difference between A and B	=2,461,000,000
Thoracic duct lymphocytes	=1,623,000,000

† Blood count A was at 3.0 p.m., hence thoracic duct lymphocytes counted from then.

(A = Commencement of experimental period. B = End of experimental period.)

Details of anaesthetic

11.35 a.m.	Chloralose 1·2 gm., saline 75 c.c.
3.5 p.m.	Chloralose 0·6 gm., saline 50 c.c.

The nature of the cells in thoracic duct lymph

The cells found in thoracic duct lymph are predominantly small lymphocytes, with so little cytoplasm that it does not as a rule appear to form a complete rim surrounding the nucleus. Some differential counts performed in the present series showed that on the average these small lymphocytes constitute 95 per cent. of the total cells. The remaining 5 per cent. consist of cells which are much larger. Some are large lymphocytes (8), others are macrophages.

When investigated by the dry smear technique these large cells may be interpreted either as lymphocytes or monocytes (*vide* Bloom (9), p. 278). Supravital staining by the neutral red and Janus green methods enables us to distinguish quite definitely between the two cell types. This method of examination shows that normal thoracic duct lymph contains no monocytes, and upon this fact all workers seem to be agreed (9, 10, 11, 12, 13, and my own results).

An accurate knowledge of the cell forms occurring in lymph is important for the following reason. The lymphocytes found in lymph may be either newly formed cells which have entered from the lymphoid tissues, or they may be lymphocytes which have entered the lymph from the blood, later to pass back into the blood. In other words, it is possible that there is a continuous circulation of lymphocytes, from blood to lymph, and from lymph to blood. The fact that we are unacquainted with any possible function which such a lymphocyte circulation might serve (the question of fat metabolism is considered further on) does not in itself prove that this circulation does not occur. Two considerations, however, are against it. In the first place 95 per cent. of the thoracic duct cells are small lymphocytes, and the small lymphocyte is generally believed to be a young and newly formed cell. Secondly the relative distribution of small and large lymphocytes is not the same in lymph as in blood. In lymph only 5 per cent. of the cells or even less are large lymphocytes. In blood about 20 per cent. of the lymphocytes are large, and the small lymphocytes usually have a better developed cytoplasmic rim than those of the lymph.

IV. THE LYMPHOCYTES OF THE BLOOD AND THEIR RELATION TO THOSE IN THORACIC DUCT LYMPH

The lymphocyte content of blood

The total white cell count per cubic millimetre of blood is carried out in the usual way, and then from the differential count the percentage of lymphocytes may be found. If the total blood volume is then ascertained, one may calculate the total blood lymphocytes. If l be the number of lymphocytes per c.mm. of blood, and v be the total blood volume in c.c., then the total blood lymphocytes $L = l \times v \times 1000$.

Relation between thoracic duct and blood lymphocytes

Under normal conditions, in spite of the fact that large numbers of lymphocytes are daily entering the blood via the thoracic duct, the number of lymphocytes in the blood remains approximately constant. This must mean that while some lymphocytes are continually entering the blood, an equal number must be leaving it, or else the number of lymphocytes in the blood would be progressively increasing, instead of remaining constant. The number of lymphocytes in the blood at any given moment is therefore the result of a balance between these two processes, some entering the blood, others leaving it. "Lymphocytosis" may therefore be due to one of two fundamentally different causes. It may be a true or active lymphocytosis, due to the entry into the blood of an increased number of lymphocytes. On the other hand it may be a false or retention lymphocytosis, owing to some interference with the mechanism whereby lymphocytes leave the blood, and their consequent accumulation in it. As an example of true lymphocytosis one may mention the lymphocytosis normally occurring in childhood, where the increased number of lymphocytes in the blood can be correlated with the presence in increased amounts of active lymphoid tissue. The term lymphocytosis as used clinically is meaningless unless we can understand which of these two processes is at fault.

The lymphocyte balance

It becomes possible, by collecting thoracic duct lymph and so preventing its lymphocytes from entering the blood, to draw up what one might term a lymphocyte balance sheet. Thus, over a given period X lymphocytes enter the blood via the thoracic duct, and X other lymphocytes leave the blood in some part of the body. Since these two processes are equal, the number of lymphocytes in the blood is fairly constant. If, however, we divert the thoracic duct lymph from the blood stream, we are preventing X newly formed lymphocytes from entering the blood. We are not, however, interfering with the X lymphocytes which leave the blood during this time. Hence at the end of the experimental period the blood should contain X lymphocytes less than it did at the commencement. In other words, the difference between the blood lymphocytes at the beginning and end of the experimental period should be of the same order as the number of lymphocytes which have been collected from the thoracic duct.

A balance sheet of this kind has been drawn up in Tables I and II. It will be seen that the figures for newly formed thoracic duct lymphocytes, and lymphocytes lost from the blood, are of the same order even though they do not exactly correspond. Over a longer period the correspondence would probably be much closer; there is further the question of the experimental error involved in all haemocytometric estimations.

Average figures for blood lymphocytes

Average figures for the total daily lymphocyte production in a 10 kg. dog have already been given (p. 252). In such a dog, taking the results obtained by Mayerson (7) on sixty healthy dogs, the following figures would be obtained for the lymphocyte balance:

Blood volume (1/13h body weight)	=770 c.c.
Lymphocytes per c.c. blood	=2,680,000
Total blood lymphocytes	=2,064,000,000
Total daily lymphocyte output (p. 250)	=5,207,000,000

Comparing then the total number of lymphocytes in the circulation with the total number of lymphocytes daily formed and passing into the blood by the thoracic duct, the significant fact emerges *that the blood lymphocytes are replaced about two and a half times daily*. In addition to this it must be borne in mind that, as previously pointed out (p. 250), large numbers of lymphocytes may enter the blood stream directly through the blood vessels of lymphoid tissue, without entering the lymph and so passing through the thoracic duct. These lymphocytes we cannot measure, but even if we disregard them entirely the figures for thoracic duct lymphocytes alone are sufficiently striking.

V. THE FATE OF THE BLOOD LYMPHOCYTES

The fundamental problem of normal lymphoid tissue

The ultimate destination of the blood lymphocytes constitutes the fundamental problem which confronts us with regard to normal lymphoid tissue. Granted that enormous numbers of lymphocytes are formed in lymphoid tissue and daily enter the blood stream, granted furthermore that equally large numbers of lymphocytes daily leave the blood, for otherwise the blood lymphocytes would not remain constant, the question presents itself "In what part of the body do these lymphocytes leave the blood, and for what purpose?"

The cell status of the lymphocyte

An essential fact which must be borne in mind is that the small lymphocyte is a young and actively growing cell. Its position is in no way comparable with that, for example, of a circulating erythrocyte. The erythrocyte is really only a dead cell remnant, and is finally broken down by the mechanical wear and tear of the circulation. Fragments of broken-down erythrocytes may be found in the blood, and also ingested by special phagocytic cells in different parts of the body. This, however, is not the case with the lymphocyte. That the lymphocyte is a young and actively growing cell is shown by its response to radiation (14). "It is generally agreed that the haemopoietic organs are very sensitive to X-rays, and that the earliest and greatest destruction occurs in the lymphocytopoietic centres." This, in conjunction with the well-known fact that the more actively growing a cell is the more sensitive it is to radiation, is

very significant. Still more important, however, in this connection is the enormous powers of development which the lymphocyte reveals in tissue cultures.

The lymphocytes in connective tissue

Normal connective tissue contains a small number of lymphocytes, and it is possible that some of the lymphocytes of the blood may leave it for the connective tissues. Our knowledge of connective tissue would not, however, lead us to suppose that it requires such an enormous supply of cells, and in any case there is evidence to show that the lymphocytes of connective tissue may multiply *in situ*, constituting the so-called histiogenous lymphocytes.

Possible sites of lymphocyte utilisation

When one considers the regions of the body which might need a regular and plentiful supply of cells, the problem narrows down considerably. The various glandular organs may be ruled out; they require a regular supply of chemical substances, but not of actual cells. The only tissue in the body which regularly manufactures large quantities of cells and might therefore be in need of constant replenishment is the bone marrow. Here, however, we are faced with the difficulty that the histological interpretation of bone marrow is extraordinarily difficult, owing to the confused and crowded arrangement of the cells. In addition, therefore, to direct histological study of bone marrow, the question has to be approached from other and more indirect angles before we can arrive at some definite conclusions.

The circulatory conditions in bone marrow

One question arises immediately: Would not the filtration from the blood stream of cellular elements require special circulatory conditions? And does the bone marrow provide such conditions? The answer to both these questions is in the affirmative. It has long been recognised that the circulatory conditions prevailing in bone marrow are peculiar, and that the alternate closing down and opening up of capillaries renders possible the escape of mature cells from the bone marrow into the blood. It does not, however, appear to have been realised that these peculiar circulatory conditions may work in the opposite way also. They not only facilitate the passage of cells from bone marrow to blood, but they also render possible the movement of cells in a reverse direction, from blood to bone marrow.

Current views on blood formation

It is interesting at this stage to consider the views now prevailing on the question of blood formation. There are two schools of thought. Both the erythrocytes and the granulocytes can be traced back to a stage in which they contain neither haemoglobin nor granules in their cytoplasm, and in which the nucleus is perfectly normal in appearance, being rounded and showing no sign

of lobulation or degeneration. This cell, with large rounded nucleus and clear basophile cytoplasm, is believed by many observers, on the basis of histological examination of the blood-forming organs, to be the large lymphocyte. These observers (Maximow, Weidenreich, and others) therefore believe that the parent cell of both erythrocyte and granulocyte is the same, namely the large lymphocyte (or lymphoid haemoblast—it has been given a variety of names in the bone marrow), and this constitutes the monophyletic theory of blood formation. Other haematologists believe that although the parent cells of the erythrocytes and the granulocytes undoubtedly resemble one another very closely, there are small but definite differences between them, and this point of view constitutes the polyphyletic theory of blood formation. As already pointed out, the histological interpretation of cell changes in bone marrow is so difficult that it cannot by itself yield an absolutely decisive answer.

The evidence of tissue culture experiments

For the elaboration of a new method of approach to the problem, we are indebted to the work of Maximow and his school. Maximow first showed that under certain (experimentally produced) abnormal conditions lymphocytes could develop into myeloid tissue in the body, e.g. in the kidney of the rabbit after ligation of the renal pedicle (15). He then showed, by a series of careful tissue culture experiments, not only that mammalian lymphoid tissue could be successfully cultured outside the body (16), but that it could give rise, through its contained lymphocytes, to fibroblasts, reticulum cells, and finally, in his later work, to typical myeloid elements (17, 18). Maximow never attempted to show that this happened as a normal physiological process in the body, but his work strongly suggests that possibility.

Very important in this connection is the work of Jordan, and Latta—work whose full significance does not seem to have been as yet correctly appreciated. Jordan (19, 20), investigating the changes taking place in lymph nodes while in the body, has shown that under certain abnormal conditions lymphocytes may give rise to abortive erythrocytes, or even complete one. Similarly, Latta (21) has shown that the lymphoid tissue in the intestinal wall of the rabbit may give rise to myeloid elements which differentiate *in situ*. It is of interest to note that Jordan, as a result of his work, was led to suggest for the lymphocyte the same life history as is put forward in the present paper.

VI. THE CONTROL OF LYMPHOCYTE PRODUCTION

Of the factors which control lymphocyte production we have no precise knowledge. Taken over a short period, less than one hour, an increased flow of lymph may result in an increased number of lymphocytes being swept into the blood, even though the actual concentration of cells in the lymph may fall (*vide* Rous (22)). Ehrlich seems to have been the first to put forward the view that an absolute lymphocytosis "is due, apart from changes in the productive

activity of the lymphoid tissue, to a flushing out of the cells through increase in lymph flow" ((23), quoted from Rous).

The injection of acid into the blood stream

The type of experiment represented by Table III is significant in this connection. The injection of 10 c.c. of *N*/10 hydrochloric acid into the circulation results in slightly increased lymph flow for 2 hours, followed by a return to normal. The cell concentration of the lymph rises steadily over the 3-hour period to more than twice its original value. It is therefore possible for an increased lymphocyte output to take place without increased lymph flow. It would appear that one of the factors causing this increased production may be a lessening of the alkali reserve of the blood.

Table III

7. vi. 32. Weight of animal 8730 gm.

Time	Lymph collected c.c.	Lymphocyte count	Hour average
2.15 p.m.	13·4	6,200	—
*3.15 „	10·6	5,800	6,000
4.15 „	15·6	7,500	6,650
5.15 „	15·5	8,560	8,030
6.15 „	10·2	13,400	10,980
7.15 „	7·5	5,700	9,500
7.50 „	6·5	8,500	7,100

* At 3.15 10 c.c. of *N*/10 HCl were given intravenously. Following this there is a steady increase in lymphocyte output as shown by the steady rise in the hourly lymphocyte count till 6.15 p.m.

Total blood lymphocytes at 1.15 p.m.	=1,972,000,000
Total blood lymphocytes at 7.55 p.m.	=394,000,000
Lymphocytes from thoracic duct	=604,500,000
Difference between blood lymphocytes at beginning and end of experimental period	=1,577,800,000

From the point of view of lymphocyte balance this table is difficult to understand. It is interesting, however, in showing the increased lymphocyte production following the introduction of acid into the circulation. The effect was *not* due to increased respiratory excursions. These did not last longer than 20 min.

If the views previously propounded concerning the ultimate fate of the lymphocyte are correct, we here have a possible explanation of the increased formation of red cells which follows anaemia consequent upon blood loss, or after the relative anaemia in people changing from a low to a high altitude. The primary response would then be the lymphocytosis, and the increased red-cell formation would be secondary. Clearly, in order to solve this problem, it is desirable to investigate lymphocyte production in experimental anaemia.

VII. THE POSSIBLE RÔLE OF LYMPH AND LYMPHOCYTES IN FAT TRANSPORT

It is generally believed that lymph and lymphocytes play an important part in the transport of fat. The evidence for this is twofold. In the first place the lymph vessels leaving the intestine become full of milky white chyle, which appears to contain a large amount of fat. Secondly, in some cases of elephantiasis, a large proportion of fat administered can be recovered from the lymph.

In neither of these two cases is the evidence entirely satisfactory. In elephantiasis we are obviously dealing with a pathological condition where the distended lymphatics may be unduly permeable, and fat may enter them in much larger quantity than normal. As far as chyle is concerned the milky white appearance is very deceptive, for the percentage of fat is astonishingly low.

A few observations bearing upon this have been made in the course of the present work. The dogs were fed at 9.0 a.m. with 225 gm. ($\frac{1}{2}$ lb.) of lard, anaesthetised at 11.0 a.m. and lymph collected from 12.30 p.m. for 7 hours. At the end of the experimental period, although no actual chemical examination of the intestinal contents was made, the small intestine was fairly empty.

In ten cases out of twelve the lymph was still white at 7.0 p.m.—10 hours after the meal. That this is not due to delay in absorption induced by the anaesthetic is shown by some observations of Rous (22), who found that in some cases the lymph was chylous when the animal was anaesthetised even 24 hours after a meal.

The total fat percentage in the three lots of lymph varied from 1·05 to 3·1 per cent. Over the 7-hour period, assuming the lymph flow to be 200 c.c.—actually it would be about 170 c.c.—6 gm. of fat would pass via the lymph into the blood.

It is possible that most of the fat had been absorbed in the $3\frac{1}{2}$ hours before the collection of lymph began. This would mean that 220 gm. of fat would have to be carried by about 90 c.c. of lymph. For as shown by Colin ((24), quoted by Heidenhain) the quantity of lymph flowing from the thoracic duct is very little affected by eating or drinking.

Some unpublished figures kindly sent me by Prof. H. S. Raper show results of the same order. In a dog fed at 9.30 a.m., chyle collected from 12.45 to 3.45 p.m. contained only 1 gm. of oil, whereas intestinal analyses showed that 18·4 out of 28 gm. had been absorbed.

Still more important from the point of view of the present work is the fact that the fat is carried in the fluid portion of the lymph, not in the cells. This is what one would expect, for the small lymphocyte, with the barest minimum of cytoplasm, is not an ideal cell for the transport of any cytoplasmic inclusion. One may therefore state quite definitely that the cells of the lymph are not concerned with the transport of fat.

VIII. THE "BARRIER" FUNCTION OF LYMPHOID TISSUE

In conclusion, it would perhaps not be out of place to consider briefly the prevailing conception of lymphoid tissue. For this conception the clinician and the pathologist are mainly responsible. The clinician and the pathologist have repeatedly observed that the lymphoid tissues are often the seat of secondary inflammation or malignant deposits. They have therefore assumed that lymphoid tissue exists for that very purpose, serving as a barrier which holds up—for a time, at any rate—the spread of injurious matter. Yet even a brief consideration will serve to show that there are serious flaws in this interpretation.

It is undoubtedly a striking phenomenon to observe a mass of lymph glands enlarged as a result of inflammation or malignant deposits. But while it is true that the lymph glands act as temporary barriers against the spread of disease, it is equally true that the lymphatic vessels greatly facilitate this spread. Thus, quite a small epithelioma on the back of the hand may cause metastases in the axillary lymph nodes; once in the lymph nodes the metastases are then held in check, albeit only for a time. Had it not been for the lymphatic vessels, however, affording these metastases an easy and rapid pathway, they would never have been able to travel as far as the axilla, but would have remained strictly localised to the hand. The gain resulting from any barrier action of the lymph nodes is more than offset by the dangerously easy dissemination made possible by the lymphatic vessels. Similar considerations apply, *mutatis mutandis*, to the lymphatic spread of inflammation.

There are other reasons which render the barrier theory untenable. Perhaps the most cogent argument against it is that the majority of people live the greater part of their lives without either acute inflammation or malignant disease. Are we then to assume that in most people the lymphoid tissues are functionless, merely marking time, as it were, until they are needed? One need merely propound this question to realise what the answer is likely to be. It is this "silent" lymphoid tissue, the lymphoid tissue occurring in the healthy organism, which we must first understand before we can begin to appreciate the meaning of pathological changes.

In the normal body the one function which we can definitely assign to lymphoid tissues is the formation of lymphocytes. It is therefore the life history of the lymphocyte which must form the starting-point of any investigation into healthy lymphoid tissue.

SUMMARY

1. Quantitative estimations have been made:
   (*a*) of the newly formed lymphocytes passing via the thoracic duct into the blood stream;
   (*b*) of the lymphocytes present in the blood.

2. From a comparison of these figures it appears that the lymphocytes of the blood are replaced on an average two and a half times daily.

3. Since the blood lymphocytes remain constant, the same number of lymphocytes must daily leave the blood as enter it.

4. Considerations are brought forward which point very strongly to the view that the lymphocytes leave the blood mainly in the bone marrow, where they develop into erythrocytes and granulocytes.

5. The factors controlling lymphocyte production are at present unknown. The results of further experiments bearing upon this will be published in a subsequent paper.

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(24) Colin (1873). *Traité de physiologie comparée*, t. ii, deuxième édition. Quoted by Heidenhain (4). Paris, p. 149.

THE EARLY DEVELOPMENT OF MAN, WITH SPECIAL REFERENCE TO THE DEVELOPMENT OF THE MESODERM AND CLOACAL MEMBRANE

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THE object of this paper is to give a short review of our present knowledge of the early stages in the development of Man, especially of the development of the mesoderm and the cloacal membrane. Although a considerable number of early human embryos have been described in the last forty years, there are still some important stages unknown and many important questions remain unsolved. There is, for instance, the question of the precise age of the known human embryos of early stages. Valuable contributions on this subject have been made by Grosser, and the reader will find all the available details in Grosser's papers of 1924 and 1927, and more recently v. Hayek (1931) and Grosser's pupil Treutler (1931) have made contributions to the solution of this difficult problem. The data thus far known, however, are insufficient to settle finally the question, in which period of the cyclic changes of the uterine mucosa the implantation of the human ovum occurs, and the length of the interval between ovulation and implantation, i.e. the duration of the migration of the human ovum from the ovary to the implantation place. Moreover we have no accurate knowledge of the details of the implantation process itself (see the different ideas described by Grosser (1924, 1927), Bryce (1924), Teacher (1925) and v. Möllendorff (1925). The lack of adequately preserved material makes it impossible to accept fully any one of these different explanations of the implantation of the human egg.

The earliest stages of the development of the human embryo so far known are already too advanced to give us an idea of the structure of the human morula and early blastocyst and of the origin of the primary mesoderm. There are several specimens described which must be considered as the earliest known human embryos. The following ova (arranged chronologically according to their description) come into consideration. Teacher-Bryce I (Bryce-Teacher, 1908; also Bryce, 1924), Kleinhans (Grosser, 1911 and 1922), SCH (v. Möllendorff, 1921*a*), Miller (Streeter, 1927) and the specimen described by Siegfried Müller in 1930. It is certain that all these specimens are much less developed than the embryo Peters (Peters, 1899 and Grosser, 1913) or the embryo Werner (Stieve, 1931), but it is very difficult to determine their exact sequence. Three

of them are very incomplete: from the series of sections through the Kleinhans ovum (Grosser, 1922) only a single section was preserved, containing only the trophoblast and the cavity of the blastocyst cut tangentially. The other sections, including the entire embryo, were lost. Of the Miller embryo there are preserved only five sections (only four of them contain the primordia of the two vesicles of the embryo), the sequence of which was not known though Streeter has been able to arrange them in their apparent serial order. Of the S. Müller specimen only three sections are preserved, one of which is suggested by the author to represent the median section.

Of the first two specimens, one (Teacher-Bryce I) was obtained by abortion and was immersed in a mixture of blood and urine 20 hours before it was fixed in alcohol. Although the preservation of the specimen is much better than one would expect from its unfavourable history, some artificial deformation of the embryo has evidently occurred. The third of the five earliest embryos —ovum SCH v. Möllendorff—shows such surprising conditions, so different from those one would expect on the basis of other known embryos that it has called forth doubts whether it is a normal ovum (see Grosser, 1924). The probability of artificial deformation is increased by the fact that the specimen is an abortive ovum.

Under such circumstances, it is really impossible to determine the developmental sequence of these five specimens: the Kleinhans ovum can hardly be discussed because of the entire absence of the embryo. The embryo SCH is somewhat doubtful because of its history and peculiar form. On the other hand, we must bear in mind that v. Möllendorff (1925) does not admit any deformation of the specimen on the ground of his own study of the sections. If he is right in this point, he is certainly justified in maintaining that the peculiar form of the embryo must not be used as a proof of the abnormality or deformation of the specimen.

The S. Müller specimen represents perhaps the youngest known stage of the development of the human embryo, but the loss of most of the sections considerably diminishes its value. Also its preservation is not perfect: the supposed primary mesoderm of the chorion is detached from the chorionic ectoderm and an extensive artificial cleft is present between them; the continuity of the chorion, adjacent to the later decidua capsularis, is interrupted by a large opening and the shrunken and detached inner contents of the blastocyst are situated in this opening. The most probable explanation of these conditions is an artificial breach of the chorionic wall and the dislocation of the inner contents of the blastocyst into this artificial opening. Such deformation can be easily explained as the result of pressure due to the mechanical damage during the treatment of the specimen or to the influence of the fixative. This explanation is supported by the great shrinkage exhibited by the specimen. On the other hand, we must call attention to the fact that if we accept v. Möllendorff's hypothesis concerning the implantation of the human egg (see fig. 18, p. 403, 1921*a* and fig. 21*a–d*, p. 36, 1925), such conditions as we can

observe in the Müller specimen (the primordium of the mesoderm plus embryo is intercalated into the trophoblast which does not cover the former on its outer surface) would be quite normal. But, quite apart from the state of preservation of this specimen, we are not prepared to accept v. Möllendorff's hypothesis without hesitation.

The specimens Teacher-Bryce I and Miller represent nearly the same developmental stage. v. Möllendorff suggested (1921*a*, pp. 369–70, 359, 384) that the Miller ovum might belong to a much more advanced developmental stage than was supposed by Streeter, and that the section published by Miller (1913) really is a tangential one. v. Möllendorff calls attention to the possibility of the existence of the connecting stalk in this specimen and thinks that the embryo in the Miller ovum is perhaps more advanced in its development than that of the ovum Teacher-Bryce I, but it is very difficult to determine what was the actual form of the latter in the living specimen because of the unfavourable conditions of preservation, or the actual size and structure of the embryo of the Miller ovum because of the incomplete series of sections. In my opinion, the trophoblast of the Miller ovum seems to be less advanced in its differentiation than that of the Teacher-Bryce I, because the network of plasmodium in the former is distinctly less abundant than that of the latter and because of the presence of a great quantity of blood in the Teacher-Bryce I specimen and the lack of blood in the trophoblast of the Miller ovum.

As was stated above, no final conclusions can be made as concerns the development of the entire embryonic primordium in these five specimens, but one fact cannot be doubted, the presence of mesoderm in stages where the primitive streak is certainly not yet present. The origin of the mesoderm in these stages must still be regarded as unknown because of the insufficiently good preservation of the specimens.

We come now to the discussion of specimens not only more advanced but much better preserved than those mentioned above. The earliest of these are the embryos Peters and Werner (Stieve, 1931). The latter was described only very briefly at the meeting of the Anatomische Gesellschaft in Breslau in 1931. Its measurements and its form show that it is certainly younger than the embryo Peters; its preservation also seems to be better than that of the latter. It is the youngest fairly well-preserved human embryo so far obtained. As I have stated above, the five earlier specimens do not admit the study of the development of the primary mesoderm because of their poor preservation. The Werner embryo is the earliest specimen where it may be suggested that at least a part of the primary mesoderm might originate from the embryonic ectoderm.

In the description of the Fetzer embryo (Fetzer-Florian, 1930, pp. 433–6) I have discussed the possibility of the existence of an area in the most caudal part of the embryonic disc where the primary mesoderm is fused with the ectoderm (fig. 3). I have suggested that we might have here before us an area where primary mesoderm originates (at least in part). This area is situated

close behind the primordium of the cloacal membrane. To this idea I was led by Prof. J. P. Hill's observations of a similar area in a very young embryo of *Hapale jacchus* (see Fetzer-Florian, 1930, p. 433). By the kind permission of Prof. Stieve I have had the opportunity of making a series of graphic reconstructions of transverse sections of the embryo Werner (the specimen is cut longitudinally), and I have used the area in question (where the ectoderm of the most caudal part of the embryonal shield is fused with the primary mesoderm and where, I suggest, primary mesoderm probably originates) for the determination of the median plane, and I have utilised also the primordium of the connecting, stalk though this is still very indistinct. The existence of the primitive streak in this stage can certainly be excluded.

Also in the Peters embryo a fusion of the ectoderm of the caudal part of the embryonal shield with the mesoderm was suggested by Graf v. Spee (Peters, 1899, p. 111), but the author did not give a further explanation of this condition. In 1909 Grosser (*loc. cit.* pp. 78–9) designated this fusion of the two embryonal layers as a "wenig deutlicher Primitivstreifen." Rossenbeck (1923), who has studied the Peters embryo very carefully and has published a series of photomicrographs of the caudal part of the embryo, expressed the following opinion: "...könnte man in der Tat daran denken, dass es sich hier um den morphologischen Ausdruck von Entwicklungsprozessen handelt, wie sie...als charakteristisch für die Primitivstreifengenese beim Menschen vielleicht angenommen werden können" (*loc. cit.* p. 360). But, according to him, this fusion could be due to the inundation of the mother by K-ions (the mother was poisoned with caustic potash) and for this reason he pronounced the Peters embryo as unfit for the solution of this question.

In the more advanced embryo Beneke (fig. 4), in which Strahl and Beneke (1910) have described a primitive groove and Strahl a head process, Rossenbeck called attention to the fact that in the region of the former there was a fusion not only between the ectoderm and mesoderm but also between the mesoderm and endoderm. Rossenbeck does not believe in the possibility of the existence of a primitive groove either in the Beneke embryo or in the embryo v. Herff (v. Spee, 1896) though v. Spee described it as present. According to Rossenbeck, v. Spee was misled by an artificial deformation, which is difficult to believe. Rossenbeck suggests that the primitive groove exists first in the Matteer embryo (Streeter, 1919) and he explains the fusion of the embryonal layers in the region in question in earlier stages as "Reste eines ursprünglich soliden Zusammenhangs im Embryonalzapfen," and the mesoderm originating from this region as a derivative of an originally solid "Mesoblastauskleidung" of the primitive chorionic cavity possibly present in the embryo SCH (*loc. cit.* p. 375).

Rossenbeck's opinion was accepted later by Grosser and v. Möllendorff. The latter originally described a primitive streak in the embryo OP (1921*b*), but under the influence of Rossenbeck's opinion explained (in 1925) the fusion of the ectoderm and endoderm in the embryos OP and WO as a

primary fusion of the germ layers or as possibly the primordium of the cloacal membrane.

In a series of papers I have tried to solve the question of the significance of this fusion. The general results at which I have arrived are as follows:

In the embryos Werner and Peters the area of fusion of the ectoderm of the caudal part of the embryonic shield with the primary mesoderm is most probably the homologue of the corresponding area described by J. P. Hill in *Hapale jacchus*. Here at least a part of the primary mesoderm originates. How extensive this part is or whether the fusion of the ectoderm with the mesoderm is primary or secondary, cannot be determined because of the lack of adequately preserved material of earlier stages. The existence of this area in later stages, as I have suggested in the Fetzer embryo and as J. P. Hill has suggested from the examination of a photograph of a section of the embryo WO (see Fetzer-Florian, 1930; Hill, 1932), must remain in doubt because of the imperfect preservation of the Fetzer embryo and because v. Möllendorff did not describe it in the embryos OP and WO.

In the embryo OP (fig. 1), the first primordium of the primitive streak is to be found in the fusion of the ectoderm with the endoderm near the end of the embryonic shield. Nothing is known about the formation of the primary mesoderm in this specimen, as was just stated above. v. Möllendorff has described an area behind the embryonic shield (in the amnion according to the author) where the limits between the ectoderm and mesoderm are indistinct and the ectoderm cells are in process of dissolution, but this area has probably nothing to do with the formation of the primary mesoderm, although it cannot be, in my opinion, quite excluded; its significance will be discussed later on p. 274.

Similar conditions with regard to the primordium of the primitive streak can be observed also in the embryo WO (fig. 2) and Fetzer (fig. 3). But already in the former I believe the first indications of the formation of the cloacal membrane can be found in the thickened endoderm area in the dorsal wall of the yolk sac underneath the caudal margin of the ectoderm of the embryonal shield, which v. Möllendorff has described as the primordium of the allantois (fig. 2, *Cl.*?). The two embryonal layers are not yet fused. In the Fetzer embryo (Fetzer and Florian, 1930), there is a distinct fusion of the ectoderm and endoderm in this region, accordingly a further step in the formation of the cloacal membrane. This fusion is situated underneath the caudal margin of the shield ectoderm and is separated from the primordium of the primitive streak by an area in which the embryonal layers are quite distinct from each other. The primordium of the primitive streak, accordingly, does not extend up to the cloacal membrane. The primitive streak and the cloacal membrane are separated also in the Beneke embryo (Florian and Beneke, 1930–1), but in this specimen (fig. 4) the development of the primitive streak is much more advanced: it no longer possesses the form of a node (as is the case in the embryo OP, WO and Fetzer), but now forms a short streak, and the formation of mesoderm is here very distinct.

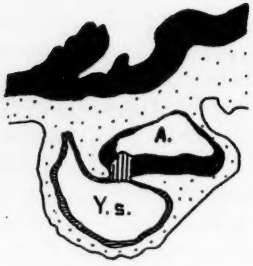

Fig. 1.

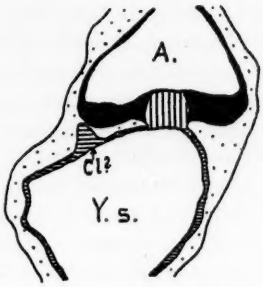

Fig. 2.

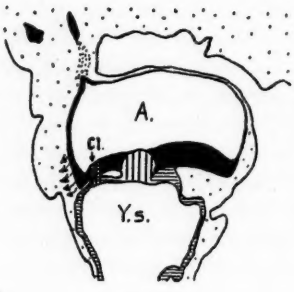

Fig. 3.

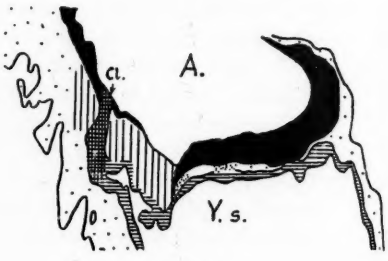

Fig. 4.

Figs. 1–8. Median sections through eight young human embryos. The cranial end on the right, the caudal end on the left: × 100. Ectoderm black; endoderm lined horizontally, head process lined obliquely, primitive streak and secondary mesoderm lined vertically. Primary mesoderm dotted.
Cl. = cloacal membrane; lined vertically and horizontally. Hensen's knot marked by crosses. *P.pl.* = prochordal plate; lined horizontally and dotted. *A* = amniotic cavity. *Y.s.* = yolk-sac cavity.

Fig. 1. Embryo OP v. Möllendorff. (Based on fig. 39, Florian, 1928.)

Fig. 2. Embryo WO v. Möllendorff. *Cl.*? = thickened endoderm in the place of later cloacal membrane. (Based on fig. 40, Florian, 1928.)

Fig. 3. Embryo Fetzer. The area caudally to the cloacal membrane where the formation of the primary mesoderm is believed to occur, marked by arrows. (Based on fig. 53, Fetzer and Florian, 1930.)

Fig. 4. Embryo Beneke. (Based on fig. 1, Florian and Beneke, 1930–31.)

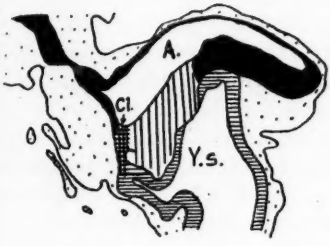

Fig. 5.

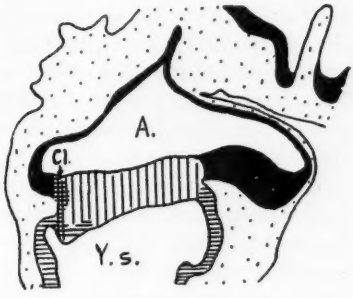

Fig. 6.

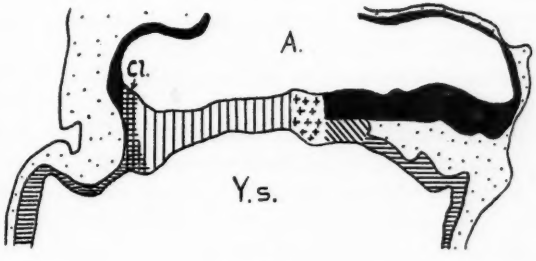

Fig. 7.

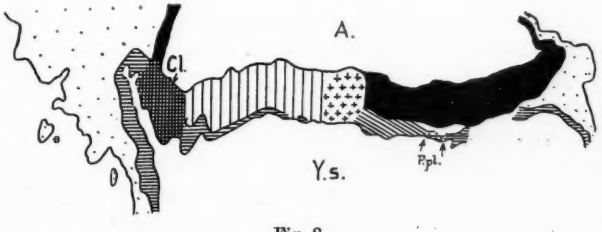

Fig. 8.

Fig. 5. Embryo Bi[ttman] I. (Based on fig. 1, Florian, 1927; somewhat altered.)
Fig. 6. Embryo T.F. (Based on fig. 43, Florian, 1928. Somewhat schematic.)
Fig. 7. Embryo "Hugo," Stieve. (Based on fig. 6, Florian, 1930*b*.)
Fig. 8. Embryo Bi[ttmann] 24.

It is very difficult to determine whether the primitive streak has reached the cloacal membrane in the embryo T.F. (Florian, 1928) (fig. 6) because of the thickness of the sections and the imperfect preservation of the specimen. In the embryo Bi I (Florian, 1927) (fig. 5), which represents a stage only slightly more advanced than the embryo Beneke and certainly younger than embryo T.F., the primitive streak does not reach the very distinct primordium of the cloacal membrane, but the distance between the two is much smaller than in the embryo Beneke.

Grosser described a new young human embryo at the meeting of the Anatomische Gesellschaft in Breslau (1931 *b*), which belongs to a stage between the embryos T.F. and Hugo. In this specimen there is a distinct fusion of ectoderm and endoderm caudally to the primitive streak and separated from the latter by an area where the columnar cells of the ectoderm of the embryonal shield are distinctly delimited from the underlying mesoderm. In my opinion, this fusion of the ectoderm of the embryonal shield with the endoderm represents the primordium of the cloacal membrane. There is nothing strange in the separation of the primitive streak from the cloacal membrane, as this is the case in the next earlier specimens. Grosser suggested that the primordium of the cloacal membrane is situated close to the caudal end of the primitive streak in this specimen, but he admits that no fusion of the ectoderm and endoderm exists in this place. The fusion which I interpret as a primordium of the cloacal membrane in this embryo would be, in Grosser's opinion, a fusion of the amniotic ectoderm with the endoderm (of the yolk sac), therefore a structure which would be comparable only with the "canalis amnio-allantoideus." The existence in Man of a structure (fusion of the ectoderm of the amnion with the allantoic endoderm) comparable with the so-called "canalis amnio-allantoideus" was first suggested by Ingalls (1918).

In later stages the primitive streak reaches the cloacal membrane (this is certainly the case in the embryo Bi 24 (fig. 8) and probably also in the embryo Hugo) and both structures become continuous. (In the Hugo embryo (fig. 7) the primordium of the cloacal membrane was not described by Stieve in the original paper, but by the kind permission of Prof. Stieve I have been able to study the sections of this embryo and have seen the cloacal membrane; see Florian, 1928, p. 545.)

In the stage of the embryo Bi 24, the cloacal membrane first exhibits the form of an actual membrane, whilst in the earlier stages it is represented by a cell cord varying in length and connecting the ectoderm with the endoderm. In all well-preserved embryos belonging to more advanced stages the cloacal membrane is distinctly present (embryos Schö, Waldeyer, 1929; Wa 17, Grosser, 1931 *a*; Kl 13, Grosser, 1913; Ho, Fahrenholz, 1927; Dobbin, J. P. Hill and Florian, 1931 *a* and *b*; Peh.$_1$-Hochstetter, Rossenbeck, 1923, etc.).

The structure interpreted by me as the primordium of the primitive streak in the embryos OP, WO, Fetzer and Beneke, as stated above, has the form of a node. The Beneke embryo is the earliest specimen in which it becomes

distinctly elongated (towards the caudal end of the embryonal shield) and so deserves the name "streak." In all more advanced specimens (beginning with the embryo Bi I) its elongated form becomes still more distinct.

Just after the formation of the mesoderm has started in the primitive streak (embryos Beneke and Bi I), probably mostly by cell migration from the ectoderm, the mesodermal cells gather underneath the caudal extremity of the primitive streak; in the embryo Beneke, we (Florian and Beneke, 1930–1) could trace the secondary mesoderm behind the caudal end of the primitive streak around the cloacal membrane into the connecting stalk. This was made possible by the fact that the secondary mesoderm in this early stage of its development was formed by very closely arranged cells, whilst the primary mesoderm possessed more the character of mesenchyme, its cells being separated from each other by more or less enlarged intercellular spaces. This observation is of importance, since it shows that the secondary or primitive streak mesoderm is not entirely used up in the formation of the embryonic body but certainly forms also a part of the connecting stalk. There is no evidence, however, that the secondary mesoderm in Man could be traced up into the chorionic membrane.

The above-mentioned accumulation of the mesoderm cells underneath and behind the caudal extremity of the primitive streak leads to the formation of a node in this place, the "end-node" (Endknoten, Florian, 1928), observed already by Stieve (1926) in the embryo Hugo and designated by this author as "Sichelknoten." This structure is to be regarded as the product of the primitive streak (see also Stieve, 1926, p. 352). It is present only in the early stages of the development of the primitive streak and very soon becomes indistinct, the cells of which it is composed assuming the character of mesenchyme. So we can understand why it was not observed in more advanced embryos than the "Hugo." In the Bi 24 the end-node is still recognisable.

If we recapitulate the chief observations stated above, we may distinguish three different areas in the caudal half of the embryonal shield in its median axis: (1) the most caudal area, differentiated in the earliest stages (embryos Werner, Peters and perhaps OP, WO and Fetzer), in which at least a part of the primary mesoderm is formed by cell emigration from the ectoderm of the most caudal part of the embryonal shield or close behind its caudal margin. (2) The intermediate area, i.e. the cloacal membrane, separated in the early stages (embryos Fetzer, Bi I, T.F., Grosser, 1931*b*), from the primordium of (3) the most cranial area, i.e. the primitive streak, which appears just before the development of the cloacal membrane (embryos OP and WO). It is not possible to determine whether the areas (1) and (2) are separated from each other or not because of the lack of adequate material. If we realise that the cloacal membrane and the primitive streak represent parts of the blastopore in lower vertebrates, we must accept the view that the homologue of the blastopore in Man originates in two separated areas which grow together only during later development. This fact has perhaps caused the difficulties in interpretation of

the structure which I regard as cloacal membrane. If we remember that the development of the caudal part of the human embryo is distinctly accelerated in comparison with the cranial part (Florian, 1930*a*), we can understand the extremely early appearance of the cloacal membrane. The precocious development of the allantois and of the umbilical stalk is another proof of this interpretation. So also is the fact to which G. Politzer has called my attention, viz. that the caudal part of the human embryo becomes elevated above the level of the embryonal shield simultaneously with the cranial end, whilst in lower Mammals the elevation of the cranial end precedes that of the caudal end. We may accordingly regard it as a characteristic of early human development that the differentiation of the caudal part of the embryonal shield is accelerated, and that in the early stages certain areas of the embryonal shield (e.g. the region of the cloacal membrane) attain a development which in lower Mammals is reached only in much more advanced stages.

It is worthy of consideration whether we may interpret also the area (1) as a part of the blastopore, but there are not enough human embryos of this stage known to solve this problem finally. This area is certainly in no connection with the earliest primordium of the primitive streak, but, on the other hand, it is in close proximity to the primordium of the cloacal membrane which is the homologue of the ventral lip of the blastopore.

There seems to be a distinct difference between the development of the primary mesoderm in Man in the region in question and the development of the connecting stalk and the exocoelom in lower Primates (*Tarsius*). In *Tarsius* there is a structure developed which may be compared with the connecting stalk in Man (Hubrecht, 1902; Hill, 1932), and the exocoelom appears in very early stages as in Man and much earlier than in other Mammals. But in *Tarsius* these two structures originate certainly in a formation which becomes a typical primitive streak (as Hill (1932) has shown; Hubrecht (1902) has designated as "ventral mesoderm" what other authors call primitive streak mesoderm), whilst in Man the site of origin of the primary mesoderm is situated behind the primitive streak, if my interpretation of the conditions in the embryo Fetzer is right.

Hill's observation on an early Hapale embryo (Hill, 1932) represents a very important contribution to our knowledge of the origin of the so-called primary mesoderm. There is an extreme similarity between this specimen (*loc. cit.* Plate 9, fig. 56) and the Werner embryo. According to Hill, we have in the *Hapale* not to do with a typical primitive streak but with a structure which precedes the latter; with this explanation I am in complete agreement. The same is, in my opinion, the case in the Werner embryo. As Hill could study only one specimen of *Hapale*, it is not possible to determine whether the fate of the region in question in later stages is the same in *Hapale* as it is in Man.

We now pass to the discussion of one fact which makes the study of the development of the mesoderm and the distinction of the primary mesoderm from the secondary mesoderm very difficult. In very many places the limits

between the mesoderm and the yolk-sac endoderm are so indistinct that the delimitation of these two layers is most difficult or quite impossible. There is evidence of fusion of the endoderm with the mesoderm of the primitive streak (at least in the median line), so that the former does not represent a distinct and independent layer (see also Rossenbeck's statements concerning the Beneke embryo mentioned in the paper of 1923 on p. 365). So it is in the earliest stages of the primitive streak before a distinct mesoderm formation takes place (see the primitive streak primordium in the embryos OP, WO and Fetzer) and during a certain period after mesoderm formation has started. I have seen this fusion of the endoderm and mesoderm in the embryos Beneke, Bi I, T.F. and Bi 24. Stieve has mentioned it in the embryo Hugo (1926, p. 355). The relations are similar to those between the endoderm and what Hill and Florian (1931 *b*) regard as mesoderm of the primitive streak accompanying the head process on both sides and cranially coming into connection with the prochordal plate. Stieve interprets this fusion between the mesoderm and endoderm as a proof of mesoderm production by endoderm and calls this mesoderm "Dottersackmesoderm." The fusion can also be observed in many places far from the median line. Fahrenholz has described (1927) a semicircular area in front of the head process in the embryo Ho, where the mesoderm is present and fused with the endoderm. Whether the "Dottersackmesoderm" really is the result of mesoderm formation from endoderm, cannot, in my opinion, be determined in sections, as there is still the possibility of a secondary fusion of the two embryonal layers.

The embryonal layers are in no place completely separated from each other by empty clefts, but are connected by means of cytodesmata. In the earliest stages they are most distinct between the ectoderm and mesoderm of the amnion and the endoderm and mesoderm of the yolk sac. The ectoderm of the embryonal shield (apart from the region of the primitive streak, cloacal membrane and the region of the formation of the primary mesoderm) is in early stages very well delimited on its under surface, often by a very distinct basal membrane (visible even in badly preserved specimens). The prolongations of the underlying mesoderm cells can be traced to this membrane. In later stages the cells of the ectoderm of the embryonal shield become connected with the underlying mesoderm cells by means of distinct cytodesmata and the basal membrane is no longer distinguishable. (For details, see Studnička-Florian, 1928, and Studnička, 1929; the latter has studied the cytodesmata between the embryonal layers in a large series of human embryos.)

In the shape of the yolk-sac and in the form of its endoderm great differences are to be observed even in very close stages (cf. the embryos Beneke and Bi I, figs. 4 and 5, belonging to almost the same developmental stage). The yolk-sac process, originally described by Strahl and Beneke (1910), has been observed (in very varying form) in many other specimens. There is as yet no consensus of opinion amongst authors as to its development. The development of the yolk-sac endoderm itself is quite unknown. We do not know whether the

yolk-sac arises as a closed vesicle or as a solid mass of endoderm, though Hill (1932) has brought forward evidence that in Selenka's Keim S of Nasalis larvatus the yolk-sac arises by the vacuolisation of an originally solid mass of endoderm. On the other hand, Stieve (1931) has advocated the view that the yolk-sac in Man is formed by the spreading of an endodermal layer as in lower Mammals.

In regard to the yolk-sac endoderm, I desire to call attention to one fact: the endoderm underneath the centre of the embryonal shield (in front of the primordium of the primitive streak) in the embryos Fetzer (Fetzer and Florian, 1930), Schlagenhaufer-Verocay (1916, p. 164) and Bi I is composed of much enlarged, vesicular cells. In the Beneke embryo (Florian and Beneke, 1930–1), there is also such an area of vesicular cells, but it is far in front of the cranial end of the primitive streak. The significance of this area is not yet determined (for further details see Hill and Florian, 1931*b*). Finally we may mention the presence of cells in the most caudal part of the yolk-sac endoderm in the embryo Bi 24, which seem to be identical with those which Politzer has designated as primary gonocytes (Florian, 1931). If these cells are really primary gonocytes, the embryo Bi 24 would be the earliest human embryo, in which they have been recognised, as in the next younger embryo (Hugo) they are not present.

v. Möllendorff called attention (1921*b*) to the presence of the "cell debris" (Zelltrümmer) situated in the amniotic cavity of young human embryos, and showed that they originate in a "Zerfallende Epithelwucherung" of the amniotic ectoderm. In his opinion the amniotic cavity (originating by dehiscence) increases in size at the cost of this "Epithelwucherung." I have tried to show (1930*a*) that the stalk ectoderm (i.e. the continuation of the ectoderm of the amnion in that region where it covers the mesoderm of the connecting stalk and which corresponds in very young stages with the "Epithelwucherung" described by v. Möllendorff) invades the mesoderm of the connecting stalk also in much more advanced stages (for instance in the embryo Bi XI with ten paired somites), and that it can eventually separate off pieces of stalk mesoderm which come to lie free in the amniotic cavity where they are finally dissolved. In the connecting stalk itself, I have distinguished two parts: the amnio-embryonal stalk and the umbilical stalk. In the same paper and partly in a paper published by Völker and myself (1929), it was suggested that the structure which was designated by other authors as "allantois" in early human embryos, really represents also a part of the hind-gut and should be called, therefore, "allanto-enteric diverticulum."

In this brief review I have dealt chiefly with the early development of the axial structures of the embryonal shield. For the accurate study of these structures the most important condition is the determination of the median plane, which is only possible after the determination of the sectional plane. I have had the opportunity to determine the sectional plane in the embryos Fetzer (Fetzer and Florian, 1930), Beneke (Florian and Beneke, 1930–1), Bi I

(Florian, 1927), T.F. (Florian, 1928 and 1930*b*), Hugo (Florian, 1930*b*) and Bi 24. I have also tried to determine the sectional plane in the embryos OP and WO (Florian, 1930*b*), but my estimation could be only very approximate, because I have had no opportunity to study the sections and the original description of these embryos does not contain sufficient figures to permit a graphic reconstruction, such as I could make in the case of the embryo "Hugo." The specimens referred to form a continuous series and make possible a detailed study of the early development of the axial structures.

It is not necessary to follow here the later stages in which the head process and the prochordal plate are established, since Hill and Florian (1931*b*) have provided a review of the development of human embryos in these stages, with references to the literature.

In conclusion, I desire to thank Prof. J. P. Hill for his great interest in my work, for his help and for reading the manuscript of this paper.

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THE POSITION OF THE VERMIFORM APPENDIX AS ASCERTAINED BY AN ANALYSIS OF 10,000 CASES

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Some twenty years ago, while a demonstrator in anatomy at King's College, I became interested in the position of the appendix in dissecting room subjects, and soon ascertained that the commonest position which this blind diverticulum of the bowel took up was a retro-caecal one. The teaching of Treves, however, was, and is at the present day, adhered to in the standard text-books of anatomy, namely that the commonest position is one in which the appendix lies in relation to the root of the mesentery and is directed upwards and leftwards pointing towards the spleen. It is a pity that this statement has not been challenged by anatomists themselves, as it is one of the rarest positions in which to find the appendix at any age from the foetus to old age.

It must be acknowledged that Treves was a great teacher and a forceful and stimulating writer, and anything that came from his pen was accepted readily without question. The cases which Treves investigated were comparatively few, certainly not sufficiently numerous to draw any definite conclusions concerning the relative frequency of the various positions in which the appendix may be found. It is quite true that the appendix may be found in almost any position relatively to the caecum, as can be seen in fig. 1, but there are many reasons why it should not commonly occupy an anterior position as Treves suggested.

The ultimate position of the appendix is profoundly influenced by the changes in position and shape which the caecum undergoes during development and growth. The caecum together with the appendix are first indicated by a simple saccular diverticulum of the gut (fig. 2, *1*), the caecal diverticulum, whereby the small intestine is demarcated from the large. After the torsion which affects the great intestinal loop occurs, the caecal diverticulum occupies a position on the right side of the abdominal cavity in close apposition with the liver. At this stage no ascending colon can be said to exist. The position of the caecal diverticulum is from the first relatively low down (caudalwards) in the abdomen owing to the precocious development of the liver which at an early stage occupies the greater part of the abdominal cavity. With the headward retreat of the liver, the caecal diverticulum and the liver become separated, one from the other, and the gut distal to the caecal diverticulum elongating,

the ascending colon comes into existence. The separation of the caecal diverticulum and the liver, or descent of the caecum, as it is inappropriately termed, is, as far as the liver is concerned, to be regarded as a relative change in position only and is due to the fact that the body wall and neighbouring parts are now growing more rapidly than the liver. As far as the body wall is concerned the caecal diverticulum for a time maintains its original position. In addition to its relative descent, however, the caecal diverticulum also undergoes an actual descent from the neighbourhood of the iliac crest into the right iliac fossa. This must be accompanied by a further elongation of the ascending colon. The descent of the caecal diverticulum relative and actual, is accompanied by changes in form. At first a simple sacculation of the gut wall, the caecal diverticulum elongates and its proximal end growing more rapidly than its distal, it assumes a conical shape (fig. 2, *2*), the caecum and the appendix not being definitely demarcated one from the other. Later, by the more rapid enlargement of the proximal and the relative constriction of the distal end, the appendix becomes differentiated from the caecum (fig. 2, *3*). With the appearance of the taeniae, the caecum, like the rest of the large gut, becomes sacculated. At first more or less symmetrical, the right caecal sacculation enlarges, while the left diminishes (fig. 2, *3*). At the same time the anterior wall which is subject to less resistance, grows more rapidly than the posterior. As a result of this asymmetrical growth, the appendiculo-caecal junction is displaced not only leftwards and upwards but also backwards (fig. 2, *4*). The factors which influence the change in form of the caecum are in the first place its actual descent into the iliac fossa—a sloping floor which tends to tilt the caecum in such manner that it occupies an oblique position with its long axis directed downwards and inwards (fig. 2, *3* and *4*). It is obvious that the right caecal sacculation must, as compared with the left sacculation, now occupy the more dependent position and is consequently subject to greater pressure from within—pressure due to the escape of the intestinal contents from the ileum into the caecum, to the gravitating effects of the erect posture on the contents of the ascending colon and to the anti-peristaltic wave which affects the proximal part of the large gut. Evidence that the actual descent of the caecum into the iliac fossa is an important factor influencing the shape of the caecum is afforded by the fact that the retention of an early form in the adult, such as a conical caecum, is more frequently found when the caecum occupies an abnormally high position, that is to say in cases where the actual descent of the caecum into the iliac fossa has failed to eventuate.

Once the asymmetrical growth has commenced, these factors will make it progress until what may be termed the extreme form of caecum may be attained, where the primitive left wall has almost or completely disappeared and the greater part of the caecum is derived from the original right and anterior walls with which part of what was primitively ascending colon may be secondarily incorporated (fig. 2, *5*). In short, during growth, the caecum may be considered to undergo a helicoidal torsion whereby the appendiculo-caecal

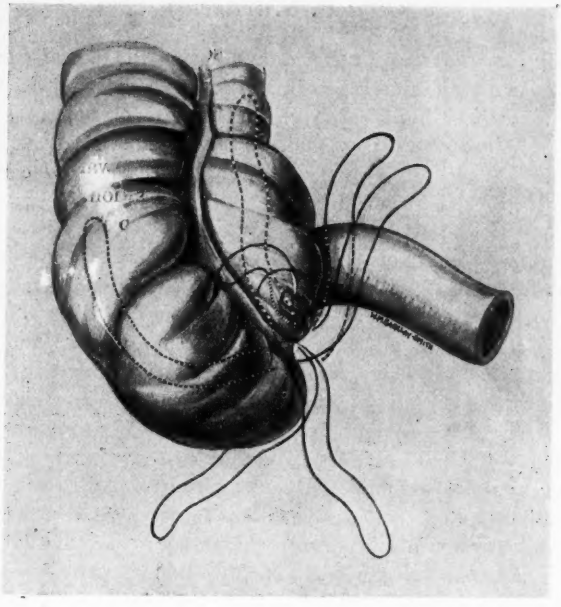

Fig. 1. Drawing showing the various positions which the vermiform appendix may occupy in relation to the caecum and terminal ileum.

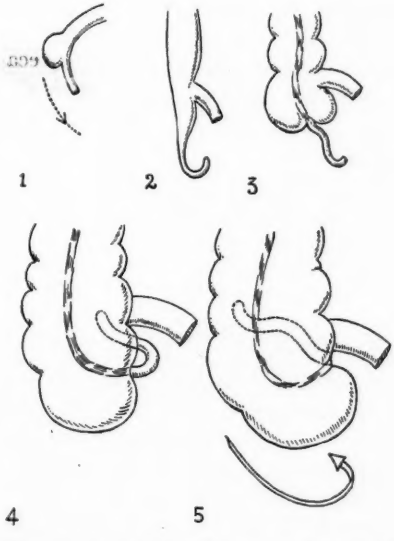

Fig. 2. Diagrammatic representation of the caecum diverticulum as it appears during different stages of development.

junction is displaced leftwards, upwards and backwards to such extent that in the extreme form it may actually lie behind the ileo-caecal junction. The method of growth of the caecum must be the main factor in determining the position of its primitively apical part, the appendix, which will be successively displaced leftwards, upwards and backwards, ultimately to lie behind the caecum which may be described as its natural position.

The position of the appendix posterior to the caecum is reflected in the disposition of its blood-vessels. The arteries to the appendix are derived from the ileo-caecal artery or sometimes from its posterior caecal branch and occupy a posterior position (fig. 3).

In the case of such a mobile part of the gut as the appendix, and taking into account the rapid and extensive changes which the neighbouring parts undergo, together with the changes in position which the appendix itself undergoes as it follows the caecum, it is obvious that it must be subject to more or less accidental circumstances which will modify its ultimate position and account for the many and various positions in which it may be found.

One of the most important circumstances modifying the ultimate position of the appendix is the urogenital ridge which may persist to a greater or less extent as the genito-mesenteric fold. The appendix, as it follows the caecum upwards and leftwards, must come into close approximation with this ridge, and will tend to be deflected downwards thereby, towards the ovary (pelvic cavity) in the female, or towards the abdominal inguinal ring in the male.

I will now proceed to consider the relative frequencies of the positions which the appendix may occupy, founded on the investigations in 10,000 cases.

Table listing the different positions which the appendix may occupy with their relative frequencies in 10,000 *cases.*

	Position of appendix	No. of cases	Percentage
1.	Anterior or pre-ileal	100	1·00
2.	"Splenic" or post-ileal	40	0·40
3.	Pelvic, or psoas muscle near or hanging over the brim of the pelvis	3101	31·01
4.	Sub-caecal beneath the "caput caeci"	226	2·26
5.	Post-caecal and retro-colic	6528	65·28
6.	Ectopic	5	0·05

THE VARIOUS SITES OF THE APPENDIX

(1) *The anterior or pre-ileal position* is rare (1·00 per cent.). The distal extremity of the appendix is directed upwards and forwards over the terminal part of the ileum. There is a long meso-appendix frequently extending up to the tip of the organ and there is often an ileo-caecal fold.

(2) *The "splenic" or post-ileal position* is even more rare (0·40 per cent.), only 40 cases being observed in the 10,000 cases examined. This is the commonest position, according to the teaching and writings of the late Sir Frederick Treves, and still quoted in most of the standard text-books of anatomy.

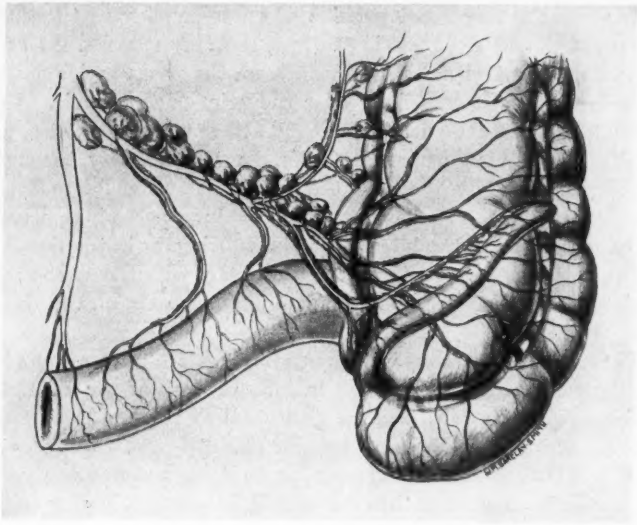

Fig. 3. The caecum and appendix from behind, showing the relations of blood-vessels and lymphatics.

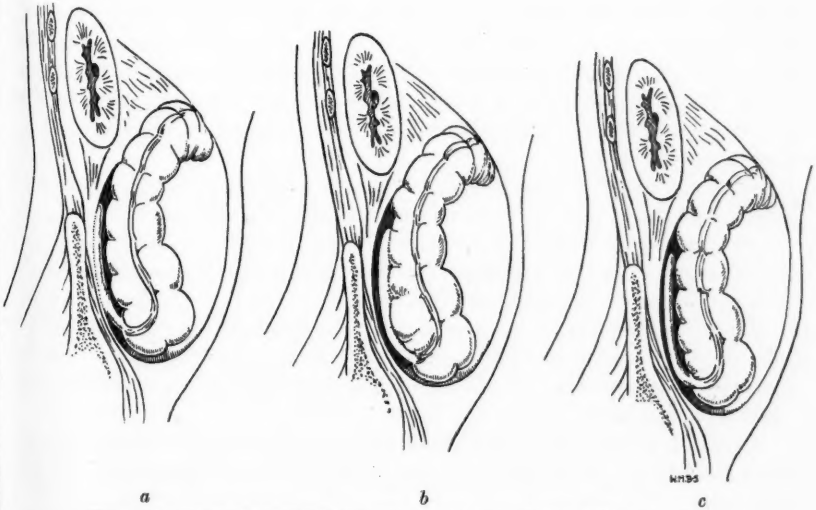

Fig. 4. Drawings showing various retro-caecal dispositions of the appendix.

When the appendix assumes this position, an ileo-caecal fold (the bloodless fold of Treves) may be present and may contain lobules of fat.

(3) *The pelvic or descending position* of the appendix is its second most common position, and was found in 31·01 per cent. of the series. As a rule, the tip of the appendix is directed downwards on the psoas major muscle and according to its length may hang over the brim of the pelvis. A genito-mesenteric fold is quite frequently present in these cases, and causes a downward kink of the terminal part of the ileum. In all probability, the position of the appendix in these cases is determined by this fold, which lies to its left side, and passes vertically downwards from the posterior aspect of the ileum or left side of the mesentery to the internal abdominal ring, or in the female to the ovary. This relationship is important in connection with the establishment of a secondary connection between the lymphatic vessels of the ovary and appendix.

(4) *The sub-caecal position* of the appendix, in which the appendix is found beneath the caput caeci, was present in 2·26 per cent. of the cases. The appendix lies on the iliac fossa and the peritoneal covering of that fossa alone separates the organ from the iliacus muscle. The appendix with its mesentery, is twisted in a clockwise direction from left to right, and frequently its tip is directed upwards. Should an ileo-caecal fold be present, it may completely cover the root of the appendix.

(5) *The post-caecal and retro-colic positions* of the appendix account for 65·28 per cent. of the cases and constitute by far the most common site. This is in accordance with the general experience of surgeons, pathologists and anatomists of the present day, but differs very markedly from the statistics which have been published by older writers and quoted in many of the English text-books of Anatomy. There are various positions in which a retro-caecal or retro-colic appendix may be found, and the following is the order of frequency:

(*a*) The appendix may be quite free, lying in a post-caecal or retro-colic pouch of peritoneum. Quite frequently, the meso-appendix is quite short in these cases (fig. 4 *c*).

(*b*) There may be a short mesentery which holds the appendix in contact with the posterior surface of the caecum and ascending colon.

(*c*) The appendix may be so adherent to the posterior surface of the caecum and colon, that together with these two structures it forms the anterior wall of a retro-colic pouch of peritoneum (fig. 4 *b*).

(*d*) The appendix may be extra-peritoneal owing to the fact that the retro-colic pouch has become obliterated, due to inflammatory processes. In such cases, any inflammation associated with an extra-peritoneal appendix may cause a perinephric abscess.

(*e*) The appendix may be quite from the posterior surface of the caecum and colon but adherent for nearly its whole length to the posterior abdominal wall (fig. 4 *a*).

(6) *Ectopic positions* of the appendix are curiosities. Five cases only were

met with in the whole of the 10,000 cases examined. In one case, there was complete transposition of the abdominal viscera. In two cases, the appendix was pre-hepatic in position, while in the two remaining cases, it was lying with the caecum in the umbilical region below the stomach and transverse colon.

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THE VERTICAL AXES OF THE FEMUR AND THEIR RELATIONS. A CONTRIBUTION TO THE STUDY OF THE ERECT POSITION

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The relations of the vertical axes of the femur to one another, as seen from the front, are most easily studied on an orthogonal tracing of the bone from the front, for the axes are readily inserted on the tracing by simple constructional procedures; and if series of bones are traced in the same standard position then comparisons may be made of the relations of their axes. The most convenient standard position in which to make the tracing is that in which the bone is placed to measure its oblique length, and in which it rests on the posterior surface of the condyles and (usually) the intertrochanteric ridge; the femur is then in the standard vertical position[1]. It is not possible, of course, to be certain that this standard position accurately reproduces in each of a series of human femora the same position relative to the position it occupied in the full extension of the standing position in the living body, for there are differences in the details of the axis of the body-weight, of spinal curvature, and of pelvic position, which will affect the antero-posterior inclination of individual bones; but apart from being small in amount, the differences in antero-posterior inclination will not affect the position of the vertical axes as seen from the front. This is also so, of course, of femora which are inclined not too much forwards, as for example the partially flexed femora of the apes. A much more important and significant difference is that which is introduced by the torsion of the femur, for it produces on the tracing a shortening of the femoral neck and, in effect, a lateral displacement of the femoral head, the amount of which will vary directly with the amount of the torsion; for if there is little torsion the neck will be almost its natural length, while if the torsion is great in amount the neck will be short on the tracing and the femoral head will be displaced laterally, as well as forwards, in relation to the lower end of the bone. This displacement of the femoral head, that is the amount of the femoral torsion, will affect the position or the direction of the femoral axes which are drawn from the femoral head to the lower end of the bone.

The tracing having been made, the infracondylar plane is drawn in on it. This plane has been assumed to be horizontal in making the further construc-

[1] The standard vertical plane of the femur is the plane tangential to the posterior surface of the condyles and the intertrochanteric ridge; it is the *horizontal* plane of the osteometer when the bone rests in the standard position on it, anterior face uppermost. (Pearson and Bell, *A Study of the Long Bones of the English Skeleton. The Femur*, p. 23. Camb. Univ. Press, 1919.)

tions; that is, it has been assumed that the latero-medial inclination of the upright bone in its proper weight-bearing position is reproduced if the condyles of the femur are placed on a horizontal plane and the bone is maintained in the standard vertical position[1]. It is obvious, of course, that in the movement of abduction at the hip-joint the medial condyle of the femur must descend and the infracondylar plane become more and more oblique; and there is a fairly general opinion that the medial condyle is at a lower level than the lateral condyle in the normal standing position[2]. It is so figured and described by Fick[3], according to whom, in standing erect on both feet with the feet apart (it is the male which is figured), the infracondylar plane slopes upwards and laterally at an angle of 3° from the horizontal and the femur is as in fig. 1. It may be calculated from the figure given by Fick that the infracondylar plane would become horizontal after a movement of adduction at the hip-joint sufficient to bring the knees together; and the femur would then be placed as in fig. 2. The relations of the anatomical axis[4] of the femur to the load axis[4] are remarkably different in the two positions, that is, there is a significant difference in the relations of the axis of the structure which is carrying the load and the "load line" of the load which is being carried. In the "Normalstellung" of Fick, the position of standing on both feet with the feet apart, the three axes of the femur intersect one another at the mid-condylar point[5], the mechanical axis being coincident with the load line and vertical in position; the axis of structure is entirely on the lateral side of the load line; and the load is equally distributed between the two condyles. In the second position (fig. 2) the anatomical axis and the load line intersect one another in the lower half of the shaft, so that the weight-carrying structure is first on the lateral side and then on the medial side of the load line of the load which is being carried; and the lateral condyle is the greater weight-bearing condyle.

[1] The articular cartilage is thicker on the medial than on the lateral condyle in 75 per cent. of (white) male femora (Ingalls, *Amer. J. Phys. Anthrop.* vol. IX, p. 355). The tracings which have been made for this study are from dried bones, which will therefore, in most instances, have taken a position slightly more vertical (0·5°–2°) than in the living subject; that is, the crossing of the load axis and the anatomical axis, which is described later, will be at a slightly higher level, and the distance between the lower ends of the axes rather more in the living subject than is shown in the tracings.

[2] This might well be held to explain the closer correlation between the maximum length of the femur and the stature than between the oblique length and the stature (see Pearson and Bell, *op. cit.* p. 5).

[3] R. Fick, *Handb. d. Anat. u. Mechanik d. Gelenke*, Bd. III, S. 522. Meyer ("Die Mechanik des Kniegelenkes," Müller's *Arch. f. Anat. u. Phys.* 1853, S. 500) definitely contradicts this statement: "Eine ganz unrichtige Angabe ist die, welche man so häufig findet, dass der innere Kondylus tiefer nach unten reiche als der aussere...."

[4] The anatomical axis of the femur is the axis of the shaft; on the tracing it passes through as many as possible of the centre points between the edges of the shaft and through the mid-condylar point. The mechanical axis of the femur is the line which joins the centre point of the head and the mid-condylar point. The load axis (or the weight line) is the vertical line from the centre point of the femoral head; it is at right angles to the horizontal infracondylar plane.

[5] Strictly speaking, it is incorrect to place the centre point of a load-carrying femur on a *curved* line, as is commonly done at the mid-condylar point; the centre point for the load should be at the centre of the *straight* line between the places where the condyles touch the infracondylar plane.

There are considerable differences in the functions of the femur in the two postulated positions. In the second position, as in standing with the knees together or with the body-weight borne on one limb in walking, the femur is acting to the fullest advantage as a static support and, if it is "locked" in this position, with the smallest requirement of assistance from the other postural organs; while in the first position, though the weight is equally distributed

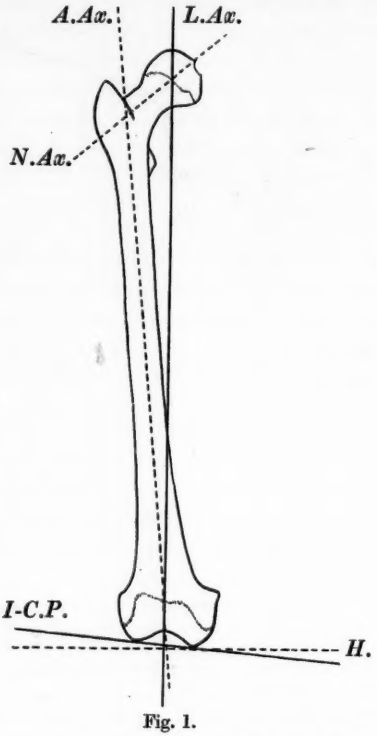

Fig. 1.

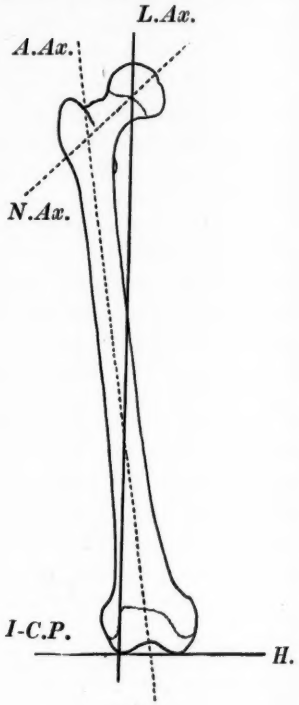

Fig. 2.

Fig. 1. The position of the femur in the "Normalstellung" (Fick). The feet are apart; the infracondylar plane slopes upwards and laterally; and the mechanical axis and the load axis coincide.
Fig. 2. The position of the femur when the infracondylar plane is horizontal. The mechanical axis is not inserted.

A.Ax., anatomical axis; *M.Ax.*, mechanical axis; *N.Ax.*, axis of neck; *I-C.P.*, infracondylar plane; *H.*, horizontal; *L.Ax.*, load axis.

between the condyles, the femur will require considerable support from the other postural organs both from its own position and to balance the medial shearing action which will be present at the knee-joint. The significance of these differences will emerge more fully later. In the meantime it may be stated that in order to confirm the position of the infracondylar plane in the two positions, X-ray photographs of the knee-joint were taken of two young adult women and

six males from 14 to 68 years of age in three different positions: (*a*) standing with the knees together; (*b*) standing in the most comfortable and effortless position with the feet apart; and (*c*) standing and carrying all the body-weight on one limb; and a wire plumb-line was placed to give a vertical line on the films. The results of this examination, omitting the differences between the right and left sides, are that in the females (statures 5 ft. 2 in. and 5 ft. 3 in.) the infracondylar line slopes upwards and medially with the knees together and is horizontal with the feet apart; in the boy of 14 and in the young male adults the line is horizontal with the knees together and slopes upwards and laterally with the feet apart; in the male aged 68 years the line is horizontal with the feet apart; and in all the line is horizontal ($\pm$ 1°) in bearing the weight of the body on one limb.

I have assumed therefore that there is a static position of the femur, as is used in walking, in which the infracondylar plane is horizontal, and a postural position of the femur in which there are individual and age and sex differences in the position of the plane. It may be pointed out here that the arrangement of the cancellous tissue in the lower end of the femur strongly suggests that the lateral condyle is the greater weight-bearing condyle, for this tissue is strongest and most perpendicular over the middle of the lateral condyle, while in a small area over the lateral part of the lateral condyle and in a larger area over the medial part of the medial condyle there is a lighter cancellous tissue and there are much larger intercancellous spaces. The suggestion is also implied in the known locking mechanism of the knee-joint, in which the terminal rotation of the medial condyle implies a stationary lateral condyle carrying the body-weight[1].

The axis of the shaft of the bone[2] is next drawn in. Often one straight line is sufficient for the whole length of the shaft, but if the bone is bowed in the latero-medial plane more than one line is required (fig. 4). The axis of the neck and the axis of the head[3] are then drawn in, and on the latter axis the centre point of the head is found at the intersection of the greatest diameter of the head drawn from the highest point on the surface of the head. The load axis is the vertical line drawn from the centre of the head, and it is of course at right angles to the horizontal infracondylar plane. On lines at right angles to the axis

[1] It is also supported, I believe, by the age changes which occur in the bicondylar widths of the femur and the tibia; namely, that there is a greater increase in the transverse width of the lateral condyles (femoral and tibial) than of the medial condyles. I have not yet collected sufficient material, however, to enable me to complete this study, but that there is a diminution in the amount of the medial projection of the medial tibial condyle from infancy onwards is recognised in orthopaedic surgery.

[2] See note 4, p. 2.

[3] Walmsley, *J. Anat.* vol. XLIX, p. 314. It is again to be pointed out that very rarely is the axis of the head a continuation of the axis of the neck as is implied in Pearson's term "capito-collar axis" (Pearson and Bell, *op. cit.* p. 19); for, usually, the axis of the head is more vertical than the axis of the neck and is inclined backwards from it, that is the head is retroverted on the neck. This retroversion of the head of the femur has since been more fully studied by Grünwald (*Zeitschr. f. Morph. u. Anthrop.* Bd. XXI, S. 103) who describes it to be, as I also think, a specific human character.

of the shaft I measured the width of the condylar masses, the width of each mass being measured from the axis to the farthest point of the mass[1].

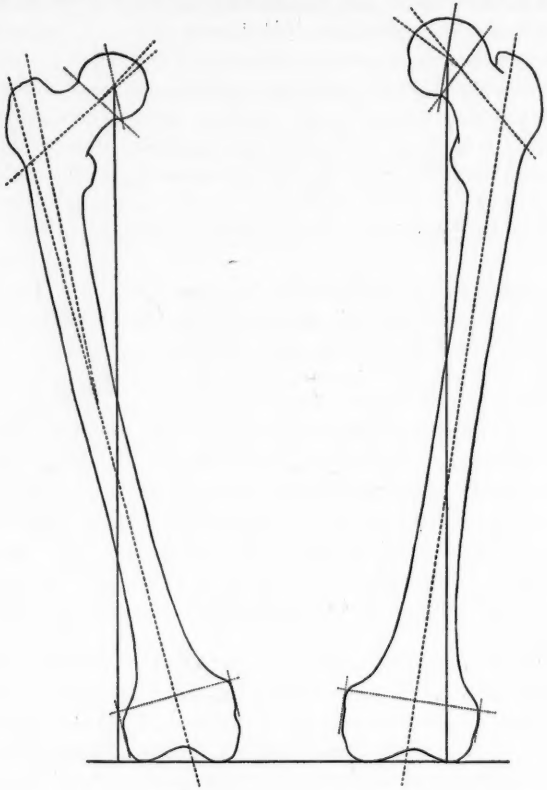

Fig. 3. Fig. 4.

Fig. 3. Modern female femur (¼ nat. size). Oblique length, 41·8 cm.; angle of inclination, 15°; angle of neck, 119°; angle of torsion, 6°; lateral condyle, 3·55 cm.; medial condyle, 3·45 cm.; shaft of femur bowed in upper part; retorsion of head absent.

Fig. 4. Modern male femur (¼ nat. size). Oblique length, 43·9 cm.; angle of inclination 9°; angle of neck, 131°; angle of torsion, 18°; lateral condyle, 3·95 cm.; medial condyle, 4·20 cm.; shaft of femur straight; retorsion of head present.

In the modern male femur the load axis crosses the anatomical axis in the lower third of the bone and passes through the lateral condyle at the place where

[1] This measurement is one which can only be used, as it is here, for gross comparative purposes, for it is a subdivision of an epiphysis by a character of a diaphysis and its variation will be affected by the variation of the diaphysis. A reliable measurement would require to be more directly related to the function of the epiphysis, but the comparative changes which are demonstrated by this measurement in the series of bones given below are of a magnitude great enough to be expressed by it. (The relation of epiphysis and diaphysis referred to here is discussed by Seitz, *Amer. J. Phys. Anthrop.* vol. VI, p. 37, and Ingalls, *ibid.* vol. VII, p. 223.)

it touches the infracondylar plane or just on the medial or the lateral side of this place (fig. 4). There is some variation in the position of the load axis, more commonly in my short series of ten bones in the lateral direction, and I have even found the axis to join the infracondylar line outside the lateral condyle; and as a rule it is more lateral in left bones than in right bones. The measurement of the medial condyle exceeds the measurement of the lateral condyle by 2·5 mm. in this bone (fig. 4), but there is a considerable variation in the proportion of the condyles measured in this way[1]; always, however, the medial condyle has exceeded the lateral condyle, and most commonly by 2–4 mm.

In the modern female femur the load line is more laterally placed than in the male, that is, it crosses the anatomical axis at a higher level and passes through the edge of the lateral condyle or even entirely lateral to it (fig. 3)[2]. The transverse measurement of the lateral condyle in this specimen exceeds the transverse measurement of the medial condyle by 1 mm.; but in the female also there is a considerable variation in the proportion of the condyles, and in my short series of ten bones the medial condyle, as in the male, was usually the larger but by a lesser amount (1–2 mm.).

In the negro male femur the position of the load axis is through the lateral part of the lateral condyle (fig. 5)[2].

The lateral condyle of the femur is thus even more the weight-bearing condyle in the female (and the negro male, Ingalls) than in the male; and this is also expressed, I believe, in the fact that the maximum antero-posterior length of the lateral condyle exceeds that measurement of the medial condyle by a greater amount in the female (and negro male) than in the male[3]. The position of the load axis, it is seen, since it is almost the same in the short (white) female and long negro male bones, is not determined simply by the length of the femur; nor are the inclination of the femur and the position of the load axis determined simply by the width of the pelvis between the acetabula, for in the negro male the acetabula are 15 mm. closer together than in the white male. It may also be pointed out here that, on mechanical principles, the higher

[1] See note 1, p. 288.

[2] This difference in the position of the load line in the male and the female is entirely in accord with the results obtained by Ingalls (*Amer. J. Phys. Anthrop.* vol. x, p. 393). He determined the position of the centre of the femoral head when projected on to the condyles, and found that in the (white) female (and in the negro male) the position was more lateral than in the (white) male. It is also in accord with Pearson's results (*op. cit.* p. 217): "The centre of the head falls externally to the mid-trochlear vertical. The amount (i.e. the distance from the mid-trochlear vertical) is absolutely greater in the female than the male...."

[3] The following figures of the maximum antero-posterior length are from Pearson's table (*op. cit.* p. 405):

	(*a*) Lateral condyle mm.	(*b*) Medial condyle mm.	$\Delta\, a-b$
London male	62·44	62·06	+0·38
London female	56·12	55·56	+0·56
Negro male	61·9	59·3	+2·6
Negro female	56·2	53·1	+3·1
Gorilla	51·2	62·7	−11·5
Chimpanzee	43·4	51·5	−8·1

crossing of the two lines—anatomical axis and load axis—permits a greater gracility of the femoral shaft in the transmission of the same load, and that herein lies the factor which determines the greater gracility of the negro femur. It is also evident that the bowing which would take place in a yielding femur

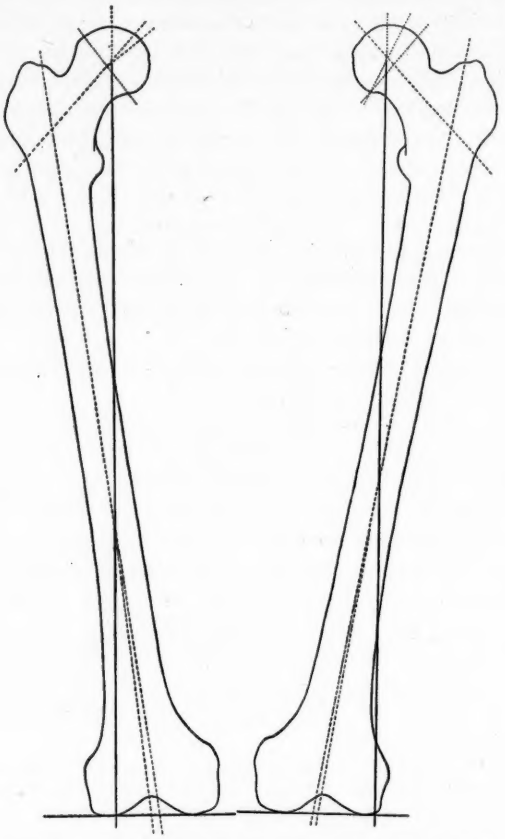

Fig. 5. Negro male femora (from the collection of Trinity College, Dublin) ($\frac{1}{4}$ nat. size).

Oblique length ...	...	Right 46·5 cm.	Left 46·6 cm.
Angle of inclination	...	7° and 9°	10·5° and 9·5°
Angle of neck ...	...	129°	126°

Shafts of both femora are concave laterally in lower parts.

would be convex laterally in the upper part, above the crossing (fig. 3), and convex medially below (fig. 5), and as does occur in genu valgum.

In the Neanderthal femora—the tracings were made from casts of the femora at Bonn and of the Spy No. 1 femur—the load axis intersects the anatomical axis at or just above the lower articular margin and passes through,

or close to, the mid-condylar point; the tendency to change from the mid-point is towards the lateral side (fig. 6). The weight of the body therefore is distributed equally, or nearly equally, on the two condyles and it is unlikely

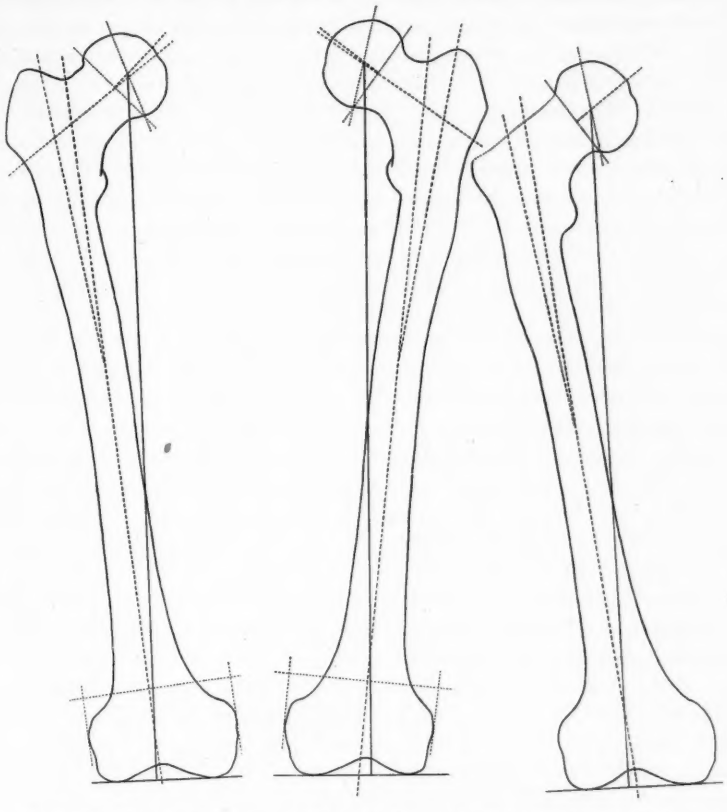

Fig. 6. The Neanderthal femora, right and left, and the Spy femur (¼ nat. size).

	Neanderthal right	Neanderthal left		Spy	
Oblique length	44·15 cm.	44·5 cm.	(44·4)	42·8 cm.	(42·85)
Angle of inclination	5·5°	6·0°	(5·5°)	7·0°	(7°)
Angle of neck	115·5°	114°	(123·5°)	—	(112°)
Angle of torsion	7°	6°	(6°)	—	(16°)
Lateral condyle	4·05 cm.	—	—		
Medial condyle	4·95 „	—	(8·96 bicondylar width)		

(The figures in brackets are the measurements given by Pearson. He measures the angle of the neck by a method which includes a character of the epiphysial head.)

that there could be a rotatory locking mechanism at the knee-joint; and this unlikelihood is strengthened by the high ellipticity of the head of the femur which would not favour the rotation at the hip-joint. The medial femoral

condyle, measured transversely from the anatomical axis, is larger than the lateral condyle by a considerably greater amount than in the modern male. The angle of inclination of the shaft is about one-half that of modern bones, that is, from the acetabulum the femora are more vertical, and at their lower ends the two bones are wider apart than modern femora are when placed on the same horizontal infracondylar plane. The Neanderthal femora correspond in position to the abduction position in modern Man when the feet are apart; that is, in Neanderthal Man the femora, lying wholly or almost wholly on the lateral side of the load axis, are not acting of themselves as static body supports but are supports which would require considerable activity of the muscles of the hip- and knee-joints. It is a safe assumption that the lower limb of Neanderthal Man was more muscular than in modern Man. The functional characters of the femur all support the conclusion of the greater muscularity of the lower limb, and at the same time are, I think, positive evidence that the bone did not function as a static support as it does in modern Man; I refer especially to the great antero-posterior bowing, the absence of pilastering, the features of the hypotrochanteric region, and the small angle of torsion. There should be added to these a further character, which is not specifically pointed out in the studies of Schwalbe, Klaatsch, or Boule, namely that there is also a bowing of the femur when looked at from the front (fig. 6). On static principles the bowing would be expected to be convex laterally in the upper part of the bones, but in the three femora it is in the opposite direction. This feature, the lateral concavity of the upper part of the femur, was not present in any other bone, Primate or human, that I have drawn; it need not be pointed out that it is not due to the great expansion of the lateral lip of the hypotrochanteric fossa there is in all Neanderthal femora, and it is, I think—like the muscular features of the hypotrochanteric region—an expression of the activity of the extensor muscles of the hip in maintaining the femur stationary in the almost erect standing position.

In the gorilla (fig. 7) the load line passes through the medial part of the medial condyle. There is a great increase in the relative size of the medial condyle, measured transversely to the anatomical axis; and the maximum antero-posterior length of the medial condyle greatly exceeds that of the lateral condyle[1]. It is the medial condyle which now bears the greater weight. The femur, relative to the position in modern Man, is in a position of even greater abduction than the Neanderthal femora; and it is to be noted in this regard that the gorilla femur does not possess the functional characters of the Neanderthal bones which indicate the use of the femur, even as a muscle supported structure, in the stationary standing position.

In the chimpanzee (fig. 8) the load line passes entirely medial to the medial condyle. The whole bone is therefore on the lateral side of the axis of weight, and as in the gorilla the medial condyle must be the weight-bearing condyle.

This group of bones, then, from the chimpanzee to the modern female (and negro male) forms a series in which there are such changes in the position of the

[1] See note 3, p. 289.

femur that there is a progressive shifting of the load line of the bone from within the medial condyle to without the lateral condyle. It remains to be determined, however, whether this series is a true continuous series and represents the changes in the form of the bone which bring about latero-medial displacement of the lower end of the femur that has taken place in the acquirement of the

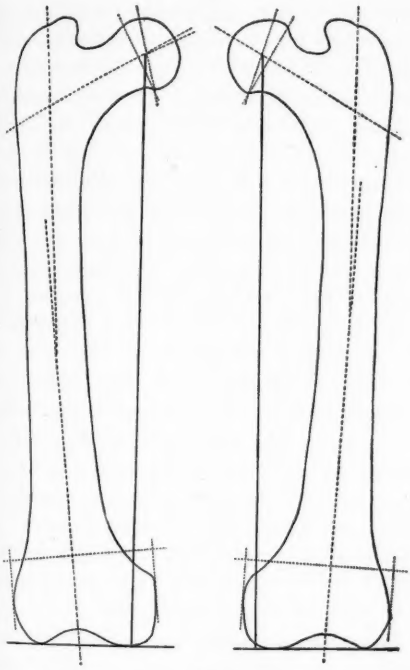

Fig. 7.

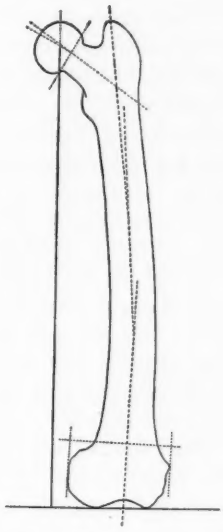

Fig. 8.

Fig. 7. The right and left femora of an adult male gorilla (¼ nat. size).

	Right	Left
Oblique length	37·45 cm.	37·5 cm.
Angle of inclination	3·3°	3·5°
Angle of neck	116·5°	119°
Medial condyle	4·9 cm.	5·15 cm.
Lateral condyle	4·0 „	3·85 „

Fig. 8. The femur of an adult female chimpanzee (¼ nat. size).

modern human upright posture. It is a matter of ordinary observation that the femur has been displaced in the latero-medial as well as the antero-posterior direction under the trunk, and under the body-weight, in the modern human posture, but that the displacement has been so far medially that the femur is in a totally new and static relation to the body-weight, and is normally in a position of genu valgum, has not been so widely recognised.

It is necessary, I think, in the first place, to recognise that a distinction should be made between the "upright posture" of the apes and the upright posture of the human subject. The former is an uprightness only in locomotion and, since locomotion is not a postural state of a balanced body but essentially involves a loss of balance and the active contraction of muscles, it cannot truly be considered to be a posture; while the latter is a true postural position, for it is capable of being maintained while stationary. All parts of the human lower limb, in this conception, are specialised for standing still upright; that is, in addition to the ape limb of locomotion, the human limb is a static support for the body-weight with the aid only of almost the smallest possible amount of the postural activity of the limb muscles. The bones of the limb are required to bear the body-weight with the aid only of the postural activity of the muscles and in the absence of their displacement contraction; and this has been accomplished by, (*a*) the bringing of the bones latero-medially under the body-weight until they cross the load line of the load to be carried; (*b*) the full extension of the thigh and leg bones vertically on one another; and (*c*) the locking of the bone most active in locomotion (the femur) in the position of medial displacement and extension at its upper and lower ends. The joint-locking mechanisms are matters of the joint ligaments and the configuration of the epiphysial articular surfaces, but the limb displacements, both from the side and the front, are primarily the result of active muscle contractions and are in fact, as nearly as possible, the terminal positions which occur, alternately in the two limbs, in upright climbing and in rapid bipedal terrestrial motion. In these activities the bones are but a small part of the supporting mechanism of transitory positions, and they do not react in their form as static structures; they are, as it were, solely for the attachment of the muscles. But when, in the human limb, as in parts of the quadruped limb, they assume static functions in the positions of extreme displacement[1] they must alter their form.

The factors which can influence the position of the two vertical femoral axes relative to one another, the infracondylar plane always being maintained horizontal, and so be concerned in the alteration of the form of the bone, are: (*a*) the amount of the inclination of the shaft; (*b*) the length of the shaft; (*c*) the size of the angle of the neck; (*d*) the length of the neck; (*e*) the presence or absence of latero-medial bowing of the shaft; and (*f*) the amount of the total torsion of the femur, in which is included the component of the retorsion. It is not necessary to describe the manner in which each of these factors acts on the position of the load axis nor, for the purpose of the present study, to analyse the changes which occur in them from the ape to modern Man[2]; but I wish to

[1] It may be expressed in the form of a paradox, that, so far as the position of the bones of the thigh and leg is concerned, the human subject stands still in the erect position with the feet together by having assumed bilaterally the position of the extreme alternate unilateral displacements of rapid bipedal movement.

[2] It will be noted that all of these factors, except for some small component of the torsion which may be an epiphysial change, are diaphysial changes; the inclination of the shaft, for example, depends very largely on the difference in the rates of growth on the medial and lateral sides of its

suggest that they are, as it were, compensatory to one another and have such a correlation that, in any form, acting together, each of them positively or negatively, they maintain the load axis in the position proper to it.

Each of these factors is a condition of the human femur which alters very greatly during the growth of the bone from birth to adult age. I therefore

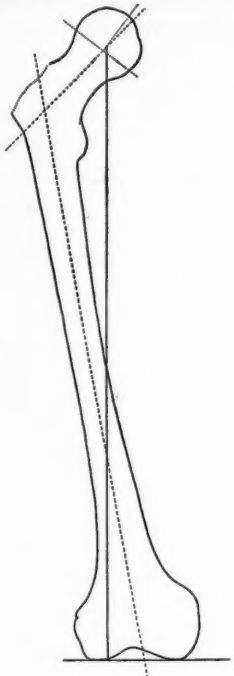

Fig. 9.

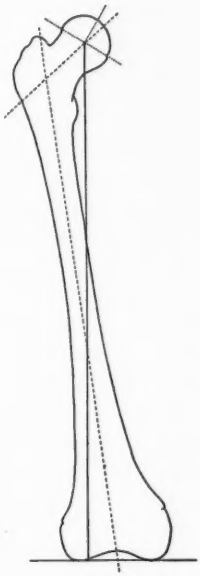

Fig. 10.

Fig. 9. The femur at 18 years ($\frac{1}{4}$ nat. size). Oblique length, 38·75 cm.; angle of inclination, 10°; length of neck, 5 cm.; angle of neck, 125°.

Fig. 10. The femur at 14 years ($\frac{1}{4}$ nat. size). Oblique length, 22·3 cm.; angle of inclination, 8°; length of neck, 3·1 cm.; angle of neck, 123°.

examined the position of the lines in a number of young femora; this would form a test, I considered, of the correlation of the activity of the factors, for the changes which occur in some of them, for example the decrease in the size of

(diaphysial) growth surfaces, and the neck of the femur is only a high specialisation of the transverse diameter of the shaft. I hope in a further communication to deal specially with the rôle of the torsion of the femur, for it is, I think, the most recent character of the modern bone and is associated with the modern upright posture. It is a means by which the head of the femur is displaced laterally over the lower end and so assists to carry the load axis from the mid-condylar position to the position through the lateral condyle; and also, at the same time, it is a means by which, as seen from the lateral side, the shaft of the femur is displaced backwards, so that the axis of the body-weight which passes behind the line joining the centres of the two femoral heads, and so extends the hip-joints, is carried in front of the knee-joints and so also effects their extension.

the angle of the neck, would displace the load line in a medial direction, while the changes which occur in others of them, for example the increase in the angle of inclination, would displace the line in a lateral direction. At 18 years of age the load line passes through the lateral condyle, and its position and its relations to the anatomical axis are as in an adult bone (fig. 9). This position and relation of the load line are maintained, I found, with a remarkable constancy in the bones I studied at 14 years (fig. 10), at 10 years (fig. 11), and at approximately

Fig. 11. Fig. 12. Fig. 13.

Fig. 11. The femur at 10 years ($\frac{1}{3}$ nat. size). Oblique length, 17·35 cm.; angle of inclination, 9·5°; length of neck, 2·9 cm.; angle of neck, 132°.

Fig. 12. The femur at approximately 3 years ($\frac{1}{2}$ nat. size). Oblique length, 13·6 cm.; angle of inclination, 8°; length of neck, 0·7 cm. angle of neck, 140°.

Fig. 13. The femur at birth (an enlarged tracing has been reduced). Angle of inclination, 6°.

3 years of age (fig. 12); so that in spite of the changes in the form of the bone the position of the load line, which seems to be defined with the onset of upright standing and walking, is most accurately maintained. At birth (fig. 13) the axes are uncrossed and the load line passes through the medial condyle. The change in position to the lateral condyle must take place between birth and 3 years of age. The position at birth certainly suggests that the series, at least from the gorilla onwards, is a continuous series and that the change to the lateral

condyle as the weight-bearing condyle is a recent human acquisition[1]. This conclusion is also indicated, I think, when the variability of the antero-posterior condylar lengths is examined. In the adult the lateral condyle is less variable than the medial condyle, but in the new-born the medial condyle is less variable than the lateral condyle; and the emphasis of this difference is increased when it is remembered that only in one other character—the inferior articular width—does the femoral variability of the new-born exceed the variability of the adult. It is as if the species character is still undefined, for the greater variability of the lateral condyle in early life I take to be an expression of its essentially human character and of the recentness of its acquisition, and that it is relatively longer, in relation to the medial condyle, than it will be in later life is, I take it, an accentuation of an early human, Neanderthaloid, character and in contrast with the Pithecoid relationship, which is the reverse.

I next made a tracing of the gibbon femur (fig. 14), and on it found that the load line has much the same position as in the gorilla. The statical conditions are more favourable in the gibbon for an upright walk with an extended lower limb than in the chimpanzee, and are such that they suggest that the chimpanzee is not part of the continuous series, but that in respect of its gait the chimpanzee is a retrogression. In *Dryopithecus rhenanus* (fig. 15)[2] the relationship of the femur to its functional requirements is, as the recent work[3] on the bones would lead one to expect, as it is in the gibbon.

The positionof the load line in *Pithecanthropus* is, as in the male negro, through the lateral part of the lateral condyle (fig. 16)[4]. In this respect also, therefore, namely the position of the bone as a functioning structure, as has so often been pointed out of its other characters, the Trinal femur is fully modern; in this respect, as in its gracility and straightness, and in the size and form of its head and of its lower epiphysis, with the two exceptions, it resembles the negro bone. In the two exceptions, the relative lengths of the condyles and the convexity of the popliteal surface, it diverges towards the gibbon (rather than towards the gorilla), but not more than some modern femora do; and it will be noted that in the relative size of the condyles, measured transversely from the anatomical axis, there is the same divergence. There is little doubt but that the Trinal femur was fully extended at the hip; the bone shows the convexity

[1] The evidence is, I think, that the change occurred in late Paleolithic time, that is, that it is present for the first time in Cromagnon Man. I have not yet been able to obtain the material for this part of this study, but I should like to point out that the Klaatsch reconstruction of the *Homo mousteriensis* (Hauseri) femur, as examined on a photograph, makes the bone to be a weight-bearing structure of a pattern akin to that of the chimpanzee.

[2] The tracing was made from the cast at the Brit. Mus. Nat. Hist. and I am grateful for the permission given me to insert it here.

[3] Gieseler, *Verh. Ges. Phys. Anthrop.* 1926, S. 34. Abel, *Die Stellung des Menschen im Rahmen der Wirbeltiere*, 1931.

[4] The tracing was made from Damon's cast. If the construction is made on Dubois' fig. 1 (a view from in front) the load line would pass further laterally and on the lateral side of the lateral condyle, while if it is made on his fig. 3 (a view from the back) the line would lie in the position it has in this tracing.

forwards of the neck, though it is only slight, the retroversion of the head on the neck, and the capsular ridge and groove on the anterior surface of the neck, which some years ago I associated with full extension at the hip in the locked position of bearing weight[1].

The results of this examination of the *Pithecanthropus* femur as a functioning structure are thus in direct opposition to the continuous series *Pithe-*

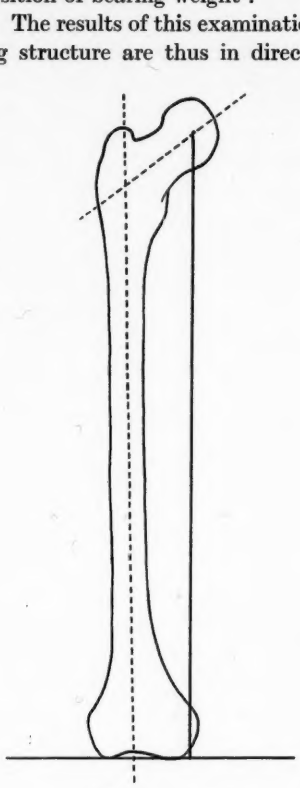

Fig. 14.

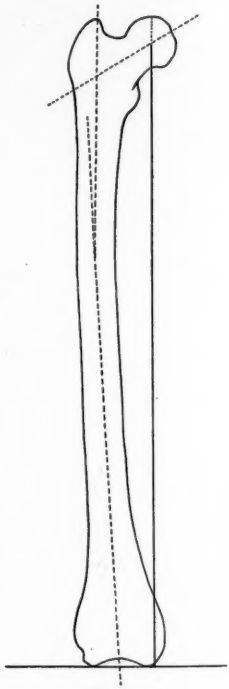

Fig. 15.

Fig. 14. The femur of the gibbon.
Fig. 15. The femur of *Dryopithecus rhenanus* ($\frac{1}{3}$ nat. size).

canthropus—Neanderthal—Recent Man, as was maintained, in respect of their gait, by Schwalbe[2], even allowing, I think, for the contention that the upright gait was not the cause but only a prop for the development of the brain, and its implication, as is contained in Dubois' position[3], that the two things, the development of the brain and the full upright human posture, might possibly

[1] Walmsley, *J. Anat.* vol. XLIX, 1915.

[2] Schwalbe maintained the sequence even in a posthumously published paper (*Zeitschr. f. Morph. u. Anthrop.* Bd. XXI, 1921).

[3] Namely, that the femur of *Pithecanthropus* has human characters because he was erect and has those characters without being human.

have occurred separately and apart from one another; and they prove that there is no justification for Bümuller's view that *Pithecanthropus* should be renamed *Hylobates giganticus*. They demonstrate, I think, that the human phylum, in respect of its gait and posture, originated in a form which, though able to be in movement with the body erect and the lower limbs well extended,

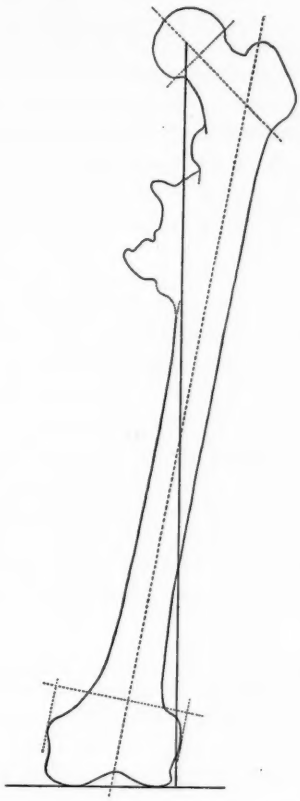

Fig. 16. The femur of *Pithecanthropus erectus* ($\frac{1}{4}$ nat. size). (The figures in brackets are the measurements given by Dubois.) Oblique length, 45·65 cm. (45·2 cm.); angle of inclination, 11·25° (12°); length of neck, 4·1 cm. (5·15 cm.); angle of neck, 124° (124°); medial condyle, 4·4 cm. lateral condyle, 3·6 cm.
(The figure given for the length of the neck shows well the effect of the torsion of 15°. The figure given for the oblique length is correct for the cast in my possession.)

was unable to stand still in the erect posture; that this form, probably through an increased rapidity of its movements in bipedal locomotion, acquired a still further extension of the femur at the hip and of the leg at the knee; and that through the fully extended position of rapid movement with the whole body-

weight being carried on and over each limb alternately, the form of the femur was so altered, at first by the growth changes which increased its latero-medial obliquity, that the load line of the bone moved laterally from the medial condyle, the bone itself assumed static functions, and standing still erect as a true postural attitude became possible. This state is represented first in the Neanderthal femora, in which, however, the static functions are still small in amount. The nearly erect standing still position of Neanderthal Man was maintained almost entirely by the activity of the extensor muscle groups: and the implication of course is that the direct line of modern human descent "has passed through the Neanderthal type or something very closely akin to it" (Pearson)[1]. The full static functions of the femur were assumed later and, as I think the evidence is, in Neanthropic Man; and was associated with the increased obliquity, the pilastering, and the increase of torsion, which are now present, and the diminution of the great bowing and of the muscular exaggerations of the trochanteric and hypotrochanteric regions which are characteristic of Neanderthal femora. There is a continuous rise of human character, as Pearson has shown, in the features of the femur from the gibbon to Cromagnon Man; and in modern femora there is a recession or, as I would prefer to consider, a refinement through a more rigid selection of the amount to their need. The femora of the modern apes do not lie within this series, for though the gorilla may be close to its commencement the chimpanzee (and the orang) are regressions from its commencement (towards quadrupedism, Morton)[2]; and, the evidence, I think, is very clear, the *Pithecanthropus* femur is modern, though there appear in it as in other modern femora features which were dominant in the earlier evolutionary stages of the bone.

I wish to thank Miss M. E. Rea for the care and the skill she has given to the making of the diagrams for this paper and which alone have ensured their accuracy.

[1] Schwalbe's discussion (*Zeitschr. f. Morph. u. Anthrop.* Bd. IX, 1906) as to whether Neanderthal Man is or is not on the direct line of descent would thus lose a good deal of its cogency.

[2] Morton, *J. Morph. and Phys.* vol. XLIII, p. 147 (1926).

THE LUMBAR AND LUMBO-SACRAL DIARTHRODIAL JOINTS

By P. N. B. ODGERS

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THIS inquiry was originally undertaken to attempt to determine whether there were any constant sexual differences in the lumbo-sacral articulation. It soon, however, became apparent that it were idle to do this without considering at the same time the diarthrodial joints of the whole lumbar column.

THE MATERIAL

As it is obviously difficult to make the measurements required accurately in articulated skeletons, 44 disarticulated lumbar columns with their corresponding sacra were collected from different sources. If this number seems small on which to base any conclusions, I must plead the difficulty of obtaining disarticulated columns with their own sacra and the fact that the method of measuring them I adopted is a most laborious one. Of these 44, 21 are modern European bones, 8 are Romano-British, while the remainder consist of ancient Egyptian skeletons from the Thebaid with one of a Patagonian. I should, perhaps, apologise for including the last, but the measurements I took from this column fall well within the limits of this series, as I understand the cranial measurements of these people do, when compared with a number of modern European skulls.

As regards the sex of these 44, 26 are considered to be male and 18 to be female. In more than half of this series the rest of the pelvis was preserved, while of the remainder in only 4 could any real doubt about the sex be entertained.

I also measured 9 infant and adolescent columns, 14 from a mixed lot of primitive races and 12 anthropoid ones.

THE MEASUREMENTS TAKEN

Previous observers have described the articular surfaces of the superior articular processes of the lumbar vertebrae and of the sacrum as looking backwards or backwards and inwards, as the case may be, but no attempt has been made previously, I think, to express these differences by any more or less accurate figures. In order to determine this varying inclination, the rather elaborate method I now describe was suggested to me by my colleague, Dr Dudley Buxton, after I had made a thorough trial of a simpler one, which

proved quite unreliable. A reference to the diagram (p. 3) will, I hope, make this method clear: here the curved lines ***AB*** and ***CD*** represent the superior articular processes.

In the case of each lumbar vertebra and sacrum investigated the following measurements were made with compasses. The maximal distance ***AC*** between the lateral borders of the superior articular surfaces and the minimal distance ***BD*** between their medial borders were first determined. Then the maximal horizontal (i.e. antero-posterior) extent of each articular surface ***AB*** and ***CD*** were measured. All these measurements were made parallel to the upper border of the corresponding vertebra or sacrum. If the minimal distance ***BD*** is subtracted from the maximal ***AC*** and the difference divided by 2, the distance ***Ab***, or rather the average of ***Ab*** and ***dC***, is obtained. Then the average value of the measurements ***AB*** and ***CD*** is found by adding them together and dividing this figure by 2. Two sides of the triangle ***AbB***, viz. ***Ab*** and ***AB***, have thus been measured and

$$\frac{Ab}{AB} = \frac{\text{Base}}{\text{Hypotenuse}} = \text{the cosine of } \angle\, BAb.$$

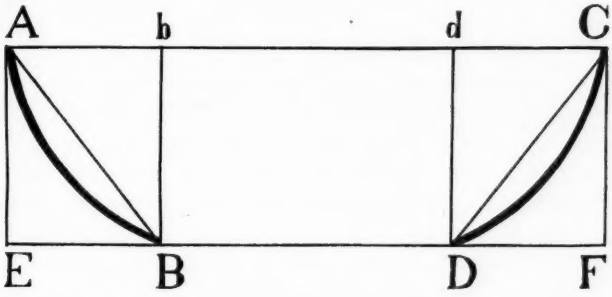
Further, as ***Ab*** and ***EB*** are parallel, $\angle\, BAb$ must equal $\angle\, ABE$. These measurements have thus given us the cosine of the angle of inclination ***ABE***, or, to express it more accurately, the cosine of the mean of the angles ***ABE*** and ***CDF***, which these superior articular surfaces make with the frontal plane. It seems more convenient, however, to express this in the terms of an index, $\frac{Ab}{AB} \times 100$, than in degrees of an angle. Such an index may be called the index of articular inclination. I shall often refer to it hereafter more simply, but perhaps less accurately, as the articular index. A concrete example may further elucidate the method. In the case of one vertebra the maximal distance between the articular surfaces $AC = 28$ mm., the minimal $BD = 18$ mm. The maximal horizontal extent of each superior articular facet = 15 mm.

Then
$$\frac{\frac{AC - BD}{2}}{\frac{AB + CD}{2}} = \frac{\frac{28 - 18}{2}}{\frac{30}{2}} = \frac{Ab}{AB} = \frac{5}{15} \times 100 = 33,$$

which is the index figure for that articulation. If, on the other hand, the articular surface looked directly backwards, the index figure would obviously be 100; the higher the index, then, the more acute is the angle which the articular process makes with the frontal plane. An index of 90 corresponds to an angle of 25°, an index of 70 to 45°, an index of 60 to 53°, one of 50 to 60° and one of 40 to an angle of 66°. With an index of over 70 the articular surfaces will appear to look more back than in, i.e. to be more in the frontal than in the sagittal plane; with an index of 60 or below, the surfaces will look

more in than back, i.e. to be more in the sagittal plane. Between 60 and 70 they would be roughly described as looking backwards and inwards.

In making my measurements I have not taken into account the varying amount of concavity displayed by the articular facets. I have in each case measured the chord and not the arc. The latter could only have been determined by the tape measure, and to this the greater accuracy and easiness of the compass method was preferred. Nor have I taken the index of each separate, right and left, articulation in any one vertebra, but the average measurement of the two. Some degree of asymmetry in the extent and in the character of the facets of a pair of articular processes—"the anomaly of the articular tropism," as Putti called it and to which Miltner and Lowendorf have more recently directed attention—is commonly seen and is not expressed in my figures.



THE LUMBAR COLUMN

If one looks at an average column (Plate I, Nos. 7 and 39), one is struck at once by the difference between the inclination of the superior articular facets in the upper two, compared with those of the lower two lumbar vertebrae. The former are looking inwards more than backwards, the latter backwards more than inwards. The third vertebra is usually the transitional one, and the facets here may follow those of the upper two (No. 39) or exhibit to a varying degree the backward inclination of the lower two (No. 7). But the lumbo-sacral column is "as variable as the individual's face" (Miltner and Lowendorf), and there is, in the first place, considerable variation in what may be called the order of maximal articular inclination. An attempt is made to show this in Table I, where the Roman numerals represent the relative positions, which each vertebra and sacrum might take, one to the other, judged by the lowness of its index of articular inclination, while the figures are the percentage frequency with which, in this series, each vertebra actually takes that place. For example, the 1st lumbar has the lowest index, i.e. its superior articular surfaces are the most inclined of any of its fellows, in 33 per cent., while it has the highest in 4 per cent. of columns, when it retains facets of the dorsal type.

Table I

	Male							Female						
	I %	II %	III %	IV %	V %	VI %		I %	II %	III %	IV %	V %	VI %
L 1	33	27	12	24	—	4	L 1	26	50	18	6	—	—
L 2	46	50	4	—	—	—	L 2	61	27	6	6	—	—
L 3	23	21	48	8	—	—	L 3	20	11	63	—	6	—
L 4	—	—	33	43	20	4	L 4	—	5	11	68	11	5
L 5	—	—	—	15	70	15	L 5	—	—	—	—	56	44
Sacrum	—	—	4	8	11	77	Sacrum	—	—	5	17	28	50

I have gone into this detailed examination of individual vertebrae to show how much the index of the same vertebra numerically may vary in different columns. If, however, an average is taken of the indices of each vertebra in all the male and then in all the female lumbar columns, the result is:

	L 1	L 2	L 3	L 4	L 5
Male	53	48	53	66	75
Female	44	43	49	58	73

If this is expressed in terms of angles instead of indices, it gives, in either sex, an average formula

$$L\,1 < L\,2 > L\,3 > L\,4 > L\,5.$$

But a glance at the photographs in Plates II and III, all of which were taken from modern European skeletons, will show that these differ from the average columns, which have been thus far considered, and very markedly from each other. The average articular index for all the 44 male and female columns together works out at 57. If one takes 52–62 inclusive as average figures, one can arrange them into three groups thus:

Between 52–62 (inclusive)	Male 12 (46 %)	Female 11 (61 %)
Above 62	„ 10 (39 %)	„ 2 (11 %)
Below 52	„ 4 (15 %)	„ 5 (28 %)
	26	18

Some years ago Goldthwait described two types of lumbar and lumbo-sacral joints, the one with flattened articular surfaces lying more in the frontal plane and the other with more or less inturned crescentic facets. He associated the former of these with a long slender flexible spine, while the second should belong, according to him, to the short thick-set heavy type of individual. Applying these suggestions, and borrowing terms which have been used to describe physical types elsewhere, I think one may call those columns with average indices below 52 hypersthenic and those with indices above 62 asthenic. Hypersthenic and asthenic columns from either sex are shown in juxtaposition for the sake of contrast in Plates II and III, and some indices of these three groups may be compared in Table II. The differences between them are, I think, sufficiently obvious to call for no further comment, while it is evident that varying degrees of motion must be permissible in the different varieties.

Table II

	No.	L 1	L 2	L 3	L 4	L 5	Sacrum	Average of lumbar column	Combined average of lumbar column and sacrum
				Male					
Average	7	39	43	63	75	88	72	61	63
	15	40	38	50	63	79	82	54	59
Asthenic	18	82	73	67	75	84	85	76	78
	2	50	52	74	86	89	68	70	70
Hypersthenic	25	32	30	40	49	78	95	43	54
	10	27	33	48	46	57	77	42	48
				Female					
Average	39	36	33	53	72	82	85	55	60
	36	38	54	62	65	79	80	59	63
Asthenic	32	44	57	67	78	77	71	64	66
	40	57	55	56	74	86	85	65	69
Hypersthenic	43	27	24	31	38	55	88	35	44
	37	35	30	37	40	53	80	39	46

THE LUMBO-SACRAL ARTICULATION

Brailsford, as the result of an analysis of 3000 radiograms of the lumbo-sacral joint, classified them thus. In 57 per cent. of cases the sacral articular facets faced backwards, in 12 per cent. inwards and in 31 per cent. were asymmetrical. The 44 sacra I have now under review can be similarly classified by taking 70 as the dividing index. This corresponds to an angle of 45° and, when the index is lower than this figure, the facets will obviously appear to be looking more in than back. The resulting percentages are very similar to Brailsford's. I found that in 55 per cent. of mine the articular surfaces looked more back than in, in 11 per cent. they looked inwards, while in 34 per cent. there was some degree of asymmetry between the two sides. Such asymmetry was very slight in the great majority of my cases, but curiously four of my photographs show it (Nos. 7, 39, 18 and 32), while in No. 25, where there is a six-piece sacrum with the interpolated vertebra only ankylosed firmly on the left side, there is gross asymmetry with a resulting marked arthritis on the right side. As I did in the case of the vertebral column, I have disregarded these asymmetries in the making of my indices for the lumbro-sacral joint. The average articular index for all the male and female sacra, of which the corresponding lumbar columns were measured, is 79 (38°). If 74–84 (inclusive) are taken as average figures, I can divide up the sacral, as I did the lumbar articulations, into three groups—average, asthenic and hypersthenic:

Between	74–84 (average)	Male	8 (31 %)	Female	6 (33 %)
Above	84 (asthenic)	„	10 (38 %)	„	6 (33 %)
Below	74 (hypersthenic)	„	8 (31 %)	„	6 (33 %)

THE LUMBAR AND LUMBO-SACRAL JOINTS CONSIDERED TOGETHER

It is interesting to see now how far there is any correlation between the index of inclination of the lumbo-sacral facets and those of the lumbar column.

Table III

No.	L 1	L 2	L 3	L 4	L 5	Sacrum	Average for lumbar column	Combined average for lumbar column and sacrum
				Male				
				(*a*) *Sacral articular index below* 74				
1	52	38	38	55	54	58	47	49
2	50	52	74	86	89	68	70	70
3	60	46	—	75	68	69	62	63
4	52	50	53	53	69	70	55	58
5	63	48	43	54	57	70	53	56
6	41	44	41	64	87	71	54	58
7	39	43	63	75	88	72	61	63
8	43	39	53	67	70	73	54	57
				(*b*) *Sacral articular index* 74–84 (*inclusive*)				
9	28	31	49	63	65	74	47	51
10	27	33	48	46	57	77	42	48
11	50	43	53	58	74	80	56	60
12	44	55	65	78	81	81	64	67
13	36	59	63	83	87	81	65	69
14	100	46	57	75	83	82	72	74
15	40	38	50	63	79	82	54	59
16	77	59	65	75	79	83	71	73
				(*c*) *Sacral articular index above* 84				
17	61	60	57	64	72	85	62	66
18	82	73	67	75	84	85	76	78
19	52	53	58	62	75	90	60	65
20	71	54	59	63	81	91	65	70
21	55	49	45	50	67	92	53	60
22	74	57	60	71	85	93	69	73
23	53	63	67	81	76	93	68	72
24	60	57	55	73	82	94	65	70
25	32	30	40	49	78	95	43	54
26	43	34	63	76	84	97	60	66
				Female				
				(*a*) *Sacral articular index below* 74				
27	37	50	44	51	79	50	52	52
28	38	46	57	62	75	61	55	56
29	55	43	65	61	69	64	58	59
30	43	41	37	50	74	69	49	52
31	45	39	48	57	73	69	52	55
32	44	57	67	78	77	71	64	66
				(*b*) *Sacral articular index* 74–84 (*inclusive*)				
33	42	41	51	56	65	74	51	55
34	50	50	47	54	77	76	56	59
35	37	30	44	56	77	79	48	54
36	38	54	62	65	79	80	59	63
37	35	30	37	40	53	80	39	46
38	62	50	50	53	73	81	57	61
				(*c*) *Sacral articular index above* 84				
39	36	33	53	72	82	85	55	60
40	57	55	56	74	86	85	65	69
41	57	65	36	41	71	85	54	59
42	50	50	58	65	88	86	62	66
43	27	24	31	38	55	88	35	44
44	52	50	59	70	78	100	61	68

Does an asthenic lumbo-sacral joint succeed an asthenic lumbar column above it or may one correct the other to some extent? In Table III the articular indices for all the vertebrae and the sacra I have so far considered are recorded and are divided into three groups in accord with the above classification of the lumbo-sacral articulations. This table shows further not only the average index for each lumbar column, but also what is called the "combined" index of lumbar and lumbo-sacral joints added up and averaged altogether, i.e. the sacral articular index is added to the sum of the lumbar indices and this figure is divided by 6. The average of the whole lot of these combined indices, male and female, is 61 and, as was done in the case of the lumbar and the lumbo-sacral articulations, one may allow 5 on either side of this mean and take 56–66 (inclusive) as average figures for the combined index. With these figures as a guide an examination of Table III shows different combinations of the two. For instance, No. 18 (Plate II) shows an asthenic sacral index of 85 accompanying an asthenic lumbar index of 76 and making an asthenic combined index of 78; or, as seen in No. 1, a hypersthenic lumbo-sacral joint (index 58) succeeds hypersthenic lumbar articulations with an average index of 47 and the combined index is hypersthenic, 49. Again, the lumbar column may correct the lumbo-sacral articulation. In No. 43 (Plate III) an asthenic sacral index of 88 is so far corrected by a hypersthenic column with an average index of 35 that the average for the lot is 44. Just the reverse of this is seen in No. 32 (Plate III). Here a hypersthenic lumbo-sacral index of 71 is combined with an asthenic lumbar index of 64 to make the final combined figure 66. The result of an analysis of this table, to show the frequency with which these different combinations occur, is as follows:

A. The lumbo-sacral and the lumbar joints are alike in 15:

Asthenic	6	5 male	1 female
Average	5	2 „	3 „
Hypersthenic	4	1 „	3 „

B. The lumbar joints correct the lumbo-sacral joint in 29:

(1) by making the combined average more hypersthenic in 15,
7 male 8 female

(2) by making the combined average more asthenic in 14,
11 male 3 female.

These facts all go to show that the lumbo-sacral and lumbar articulations cannot be fairly considered separately. I do not think that the conditions, which obtain in these joints, are emphasised in any ordinary anatomical description of them, although they were pointed out by Struthers years ago, and are not, I venture to think, sufficiently appreciated by surgeons. von Lackum, for example, wrote: "In the lumbar region rotation is checked by the articular processes lying in the sagittal plane. At the lumbo-sacral junction an attempt is made to increase motion by adding more or less rotation. This added rotation jeopardises the joint." Or Putti: "The articular facets of

the first four lumbar vertebrae are placed on the sagittal plane, while those between the fifth lumbar and first sacral are on the frontal plane." Any such abrupt change at the lumbo-sacral junction is exceptional. In the first place, as has been seen above, in Table I, the sacrum does not take by any means always sixth place in the order of degree of articular inclination. Secondly, if it be allowed that a difference of over 15 in the relative indices of the 5th lumbar and sacral facets may be regarded as denoting a more or less sudden change in the angle of inclination, it is perhaps surprising to find that such a difference only occurs in a quarter of the columns now under review—in 11 out of 44. Moreover, in 4 of these 11 the change is the other way round, the sacral articular index being the lower. Nos. 25 and 43 (Plates II and III) are good instances of such an abrupt change from hypersthenic lumbar to an asthenic lumbo-sacral joint, while No. 7 (Plate I) exemplifies the opposite condition. Rather, as I hope a consideration of the indices has already shown, is there in the great majority of cases a gradual opening out of the three lower pairs of the superior lumbar facets from the sagittal towards the frontal plane. The text-book type of lumbar articular process, which begins almost always with such abruptness at the dorso-lumbar junction, becomes less and less pronounced below the 2nd lumbar vertebra, and with this change there must be the possibility of some rotatory movement in the lower lumbar column. While there is some sexual difference, to which I shall refer presently, if all the figures for these 44 columns are analysed and any index of 70 or over (70 = 45°), a figure which errs, I consider, on the safe side, is presumed to allow of some amount of rotation at those joints, I find that this may occur in the lower 3 articulations in 2 per cent. of columns, in the lower 2 in 32 per cent., while it is confined to the joints between the 3rd and 4th lumbar vertebrae in 2 per cent., to those between the 4th and 5th in 41 per cent. and cannot occur at all in the lumbar column in 23 per cent. The question of the possibility of rotation occurring in the lumbar column has been a matter of great argument among anatomists from time to time, and these observations of mine all go to support the older view of Henke, Meyer and Morris.

Taking the same index of 70 as a guide, there are 8 lumbo-sacral articulations (18 per cent.), where no rotation can presumably occur. This is compensated for by the joints of the lower column in all but two cases; in these (Table III, Nos. 1 and 29) apparently no rotatory movement is possible at all, either in the lumbar column or at the lumbo-sacral junction.

SEXUAL DIFFERENCES IN THE DIARTHRODIAL JOINTS

If the average articular indices of the consecutive vertebrae in male and female lumbar columns are compared, differences in every instance are at once apparent.

	L 1	L 2	L 3	L 4	L 5	Sacrum
Male	53	48	53	66	75	81
Female	44	43	49	58	73	76

To prevent conclusions being drawn from what was perhaps too small a number of measurements, Dr Buxton was good enough to examine my figures from the statistical standpoint and has proved them to be of significant value. The average of the articular indices for all the male columns works out at 59, contrasted with a female average of 54. If the same thing is done for the lumbo-sacral joints, the male average is 81, the female 76, or, if the articulations of the lumbar column and sacra are considered together, the male combined average index is 63 to that of 58 for the opposite sex. All these figures suggest that the female lumbo-sacral and lumbar joints tend to be more hypersthenic than those of the male and I found in fact that, while the male series showed only 15 per cent. of the hypersthenic type to 39 per cent. of the asthenic, in the female set there were 28 per cent. of hypersthenic to 11 per cent. of asthenic columns. By the same token, it is interesting to note in this collection the cases of lumbarisation of the superior articular facets of the 12th dorsal vertebra. This was seen on both sides in 4 out of 18 female columns, but only twice in 26 male columns, while it was unilateral in 2 females and 2 males—a percentage incidence on one or both sides of 33 per cent. for females and 15 per cent. for males. Curiously this lumbarisation was only noticed on one side in 2 modern skeletons; all the other examples appeared in Romano-British or in ancient Egyptian bones. In contrast to this the only instances of the superior articular facets of the 1st lumbar vertebra remaining dorsal in type, unilateral in one and bilateral in a second, occurred in modern male vertebrae. This hypersthenic tendency of the female column must allow less potential rotation than may occur in the male. The two can be contrasted thus, where the figures represent the percentage frequency of possible rotation at different vertebral levels, with the index of 70 used again as the discriminating figure, while the numbered vertebrae are abbreviations for the corresponding superior articulations, e.g. L 3 means the diarthrodial joint between the 2nd and 3rd lumbar vertebrae:

	L 3	L 4	L 5	L 4 L 5	L 4	L 5	None
Male (%)	4			38	4	31	23
Female (%)	0			22	0	56	22

That the possibility of rotatory movement should be confined so frequently to the joint between the 4th and 5th lumbar vertebrae would seem to be a female characteristic, and this must be correlated with the fact that in half the female columns under review the 5th lumbar shows a higher articular index than the corresponding sacral facets do (Table III).

Lastly, one other sexual difference may be briefly indicated. The average formula given above, L 1 < L 2 > L 3 > L 4 > L 5 > S, is followed exactly by 33 per cent. of female, but only by 19 per cent. of male columns: this suggests a greater constancy in the make up of the former.

PRIMITIVE RACES

I thought it might be interesting to compare the articulations I am considering as seen in some primitive people with my original series. In all 14 columns with their sacra were measured, which came from aboriginal Australian, Bushman, Andamanese and Melanesian skeletons. The indices for these are set out in Table IV, where those marked with an asterisk were measured

Table IV

No.		L 1	L 2	L 3	L 4	L 5	Sacrum	Average index lumbar column
				Male				
1	Australian aborigine	50	51	42	50	61	72	50
2*	,,	46	58	44	68	—	89	54
3*	,, (aged 18)	50	61	46	69	75	67	60
4*	,,	72	54	53	69	69	65	63
5	Andamanese	45	57	64	80	89	85	67
6	,,	47	48	58	80	82	96	63
Average for each vertebra		52	55	51	69	75	79	
				Female				
7	Australian	63	35	52	54	76	84	56
8*	,,	68	52	64	61	68	65	63
9	Bushman	92	33	41	56	80	76	60
10†	,,	40	35	44	62	88	90	54
11	,,	71	45	36	52	64	81	54
12†	Melanesian	95	93	57	78	89	80	82
13	Andamanese (aged 19)	65	58	70	70	72	79	67
14†	,,	38	30	47	74	82	88	54
Average for each vertebra		66	48	51	63	77	80	

† In No. 12 the right superior articular facet of the 12th Dorsal vertebra is lumbarised. In Nos. 10 and 14 this lumbarisation is bilateral.

in articulated columns: this is obviously more difficult and less accurate. The following are briefly the points to be noted wherein these differ from those analysed already.

(1) If 74–84 is again adopted as the range of average index figures, of these male lumbo-sacral joints 3 are hypersthenic and 3 are asthenic: of the female 5 are average, one is hypersthenic and 2 are asthenic in type.

(2) If one takes 52–62 again as the range for the average lumbar indices, one finds 2 of these male columns are average, one is hypersthenic and 3 are asthenic: of the 8 females 5 are average, 3 are asthenic but none are hypersthenic.

(3) A reference to the average figures of the individual vertebral indices shows that the 3rd lumbar has the smallest index of any in the male column, while in the average formula for my original series this belongs to the 2nd lumbar. There is no change of order in the female column.

The conclusion one may perhaps draw from this small number of obser-

vations is that, while there is little difference in the sacral articular indices—the male average is 79, the female 80—the tendency is for male and female figures to approximate by reason of the comparatively asthenic type of the lumbo-sacral joint in the female. This becomes more noticeable still, when the figures for the lumbar columns are considered. Here they work out at 60 for the male and 61 for the female average indices, compared with 59 and 54 respectively in my first series. This asthenic tendency in the female lumbo-sacral and lumbar joints with the consequent decrease in sexual difference is at least remarkable.

THE LUMBO-SACRAL AND LUMBAR ARTICULATIONS IN THE ANTHROPOIDS

Table V shows some measurements made on a small number of gorilla, orang, and chimpanzee lumbar columns with their sacra. Those marked with

Table V

No.		L 1	L 2	L 3	L 4	Sacrum	Average for lumbar column
			Gorilla				
1*	♂	96	85	76	61	35	79
2*	♂♀	92	92	85	—	61	90
3	♂♀	93	80	73	—	74	82
4*	♀	62	63	47	32	25	51
Average for each vertebra and sacrum		86	80	70	46	49	
			Orang				
1*	♂	78	75	80	82	73	79
2	♂♀	73	87	79	80	97	80
3	♂♀	96	75	80	81	78	83
4	♀ (young)	100	100	100	93	93	98
Average for each vertebra and sacrum		87	84	85	84	85	
			Chimpanzee				
1*	♂	50	39	29	—	43	39
2	♂♀	79	56	58	58	59	63
3	♂♀	65	58	50	47	37	55
4*	♀	61	62	58	58	55	60
Average for each vertebra and sacrum		64	54	49	41	48	

an asterisk were in articulated skeletons. A consideration of these figures brings out the following facts.

(1) As Struthers pointed out, the pyramid in the lumbar column is reversed. In Man the base is, of course, below, while in the gorilla or in the chimpanzee the base is above. In both the latter the articular index decreases in a more or less regular fashion from above downwards and the sacral articular index is the lowest in practically every case. In the orang there is little alteration in the average figures either between the successive vertebrae or between the vertebrae and the sacrum.

(2) The very high average indices of the lumbar articulations in both the gorilla and the orang—that for the gorilla is 75, that for the orang 85—suggest much greater potential mobility and certainly greater instability, when compared with the corresponding indices for the human column.

(3) Any sexual difference is very slight. If the measurements for the gorilla and orang lumbar columns are considered together, the average index for the male is 81, for the female 78. This latter figure is augmented by the inclusion of the young female orang and yet indicates a tendency for the female column to be less asthenic than the male.

(4) The chimpanzee stands out with an entirely different set of figures to those of the gorilla or the orang. The average index for the vertebrae works out here at 54—the only male included has the lowest average—and is the same as that of the female columns in my original human series. I believe the chimpanzee is said to be the best quadruped of these three anthropoids (Sonntag), while the gorilla is the most human in its method of locomotion (Keith).

POSSIBLE FACTORS IN THE CAUSATION OF THESE DIFFERENCES IN THE LUMBO-SACRAL AND LUMBAR JOINTS

(1) The first question to be very shortly considered is whether there is any correlation between the shape and size of the vertebral bodies or of the base of the sacrum and the inclination of the articular facets. To take the lumbo-sacral joint first. Without entering unnecessarily into an old controversy, I think there is ample evidence that the first piece of the sacrum is the last to be thoroughly sacralised (Speransky). Can one say, then, that the more the latter is the case, the less lumbarised will be the inclination of the articular processes? In attempting to answer this question I measured 44 sacra in addition to those of my first series, giving me a total of 88; of these 46 were male and 42 were female. In these 88 I determined not only the index of articular inclination, but also the following:

(*a*) The amount in millimetres of hypo-, homo, or hyperbasality (Radlauer). The deeper the first piece of the sacrum sinks into the sacral mass, the more it loses its lumbar characteristics (Speransky).

(*b*) The upper "querkrümmungs" index (Radlauer, R. Martin). This is the $\frac{\text{upper straight breadth} \times 100}{\text{the upper curved breadth}}$. The higher this index, the flatter is the transverse curve and presumably the more sacralised is the first sacral vertebra. Radlauer suggested that the direction of the articular surfaces depends on the degree of the transverse curvature of the sacrum.

(*c*) The transverso-sagittal index of the superior surface of the body of the 1st sacral vertebra, i.e. $\frac{\text{the greatest sagittal breadth} \times 100}{\text{the greatest transverse breadth}}$. The wider the body compared with its depth, the lower is the index and presumably the

more sacralised the vertebra. In the table this is called the body index. The result of this investigation is seen in Table VI, where the figures represent average indices. The sacra were divided into the same three grades as previously, an average group with indices between 74–84 inclusive, a hypersthenic group below 74 and an asthenic group with indices above 84. The briefest survey of this table shows that there is no sign of any sort of correspondence between the different figures. The same negative result is obtained, if one attempts to correlate the articular index in the lumbar column either with the increasing width of the vertebral bodies or with the minimal distance between the pedicles.

Table VI.

	Male				Female			
	Average articular index	Average hypobasal. in mm.	Average querkrüm. index	Average body index	Average articular index	Average hypobasal. in mm.	Average querkrüm. index	Average body index
Hypersthenic	68	9	94	60	65	6	94	63
Average	80	11	93	61	80	6	94	59
Asthenic	90	11	93	59	90	7	95	60

Table VII.

No.	Sex and age in years	L 1	L 2	L 3	L 4	L 5	Sacrum	Average for vertebrae	Combined average	Mammillary tubercles
1	Female 1¼	90	100	100	100	100	96	99	98	—
2	Female 4	54	38	50	57	—	82	50	56	+
3	? 6	100	—	71	87	87	—	86	—	—
4	Male 8	75	59	79	100	100	94	83	84	—
5	Male 9	57	75	85	96	94	100	81	84	—
6	Male 12	45	47	67	67	87	88	63	67	+
7	Male 14	50	57	54	68	78	72	61	63	+
8	Male 15	58	54	55	81	96	100	69	74	+
9	Male 18	23	35	39	59	60	80	43	49	+

(2) *The development of the articular inclination.* Table VII shows the articular index in the individual lumbar vertebrae and in the sacrum at nine different ages. All of these columns were disarticulated; 6 came from male children and 2 from female, while the sex of another was unknown owing to the absence of the sacrum. The average for each lumbar column shows a regular decrease from infancy to adolescence, if No. 2 is excepted. The measurements in the latter seem quite extraordinary. It is said to have come from a child of 3 years old, and its maximum age cannot be more than 6, and yet it already exhibits in two vertebrae articular facets of a hypersthenic type and has an average index of 50. May this possibly be an early expression of its sex? At 15 months, the youngest I investigated, the articular surfaces are practically flat and all look directly backward, while even at 8 years (Plate IV, fig. 1) the average index is as high as 83. I confess these measurements of mine are rather difficult to reconcile with Bardeen's statement, that as early as the 50 mm. stage "in the lumbar region the superior articular processes

develop faster than the inferior with the result that each superior process comes partly to enfold the inferior process of the vertebra next anterior." The last point to which attention may be directed in this table is that the mammillary tubercles are not seen as a rule before about 12 years of age. Before this they are of course almost entirely cartilaginous and are lost from the dried bones. They are, however, quite obvious, tipped with cartilage, in the precocious specimen No. 2, to which I have already referred.

(3) *The mammillary tubercles.* Any series of lumbar columns and sacra will show that these tubercles are variable both in their size and in their relation to the superior articular facets. I noted their condition in 88 sacra and I found that, if I divided these up into my three groups, that those with average indices showed well-marked tubercles in 40 per cent. of males and in 50 per cent. of females; those hypersthenic in type had good tubercles in 86 per cent. of males and in 77 per cent. of females, while in the asthenic variety they were only seen in 8 per cent. of males and in 9 per cent. of females.

A study of the photographs in Plates I, II and III reveals that in the lumbar column three different conditions of these tubercles may be observed.

(*a*) No. 18 (Plate II) is a photograph of a male asthenic column with very poorly marked tubercles practically throughout.

(*b*) Both male and female average columns (Nos. 7 and 39, Plate I) show well-developed tubercles, particularly in the upper three vertebrae. Again, the female asthenic column (No. 32, Plate III) has good mammillary processes throughout, but the point, to which I would draw attention, is that in all these three instances the tubercles, even where they are best marked, are separated from the superior articular surfaces by a definite sulcus.

(*c*) Very different from either of these two preceding groups is the condition of these tubercles to be noticed in the photographs of hypersthenic columns (Nos. 25 and 43, Plates II and III). Here they may be less obvious than in No. 32, but here they definitely involve the postero-lateral border of the articular surface instead of being separated therefrom.

One can observe one of these three conditions of mammillary tubercle running all through the different series of columns I have measured, both human and anthropoid, so that in any individual vertebra one can safely associate backward-looking articular surfaces with a poor development of this tubercle or, if it be well marked, with one divorced from the joint, while in the case of facets well inturned towards the sagittal plane, one can look with assurance for well-marked tubercles actually contiguous with the articular surface. As a corollary to this, these tubercles are best developed in nearly all columns in the upper two or three lumbar vertebrae (Nos. 7 and 39, Plate I; No. 25, Plate II).

(4) *The multifidus spinae muscle in the lumbar region.* Several years ago H. Virchow accurately described this as a multipennate muscle of the greatest complexity with superficial and deep tendons. My own dissections confirm what he wrote. Directly the lumbar portion of the muscle is cleanly exposed,

the difference between its upper and lower halves is strikingly evident. In the upper half constantly three, or less often, four discrete superficial tendons stand out in the general fibrous sheath and are seen to arise from the corresponding three or four mammillary tubercles. In the lower half, where the muscle is more substantial, no such appearance is presented. If the muscle is dissected, deep to these superficial tendons, muscle fibres are found arising both from their medial surface and from the mammillary tubercles as well as from a deeper series of smaller tendons. In the lower half of the muscle these deeper tendons, like the superficial ones, are wanting.

(5) *Conclusion.* The mammillary tubercles are only muscular processes for the origin of the multifidus and their size must vary with its degree of development. Further, in this connection I would particularise the deeper musculotendinous lamina of the muscle, so well marked in the upper half of the lumbar region, as being peculiarly responsible for the mammillary ossification involving the articular border. Such involvement can be observed very prettily in those cases of unilateral lumbarisation of the superior articular facets of the 12th dorsal vertebra. There are photographs of two instances of this (Plate IV, fig. 2). Here the superior tubercle of the transverse process can be seen on the one side to be spreading on to and catching up the lateral border of the articular surface, while on the other the tubercle stands out distinct from the articular surface, which keeps its flattened dorsal inclination.

The gradual increase in the angulation of the articular surfaces during infancy and adolescence, their varying closeness of connection with the mammillary tubercles and the variable size of the latter, together with the anatomy of the multifidus muscle all seem to me to be regular steps in the argument, which points to the conclusion that it is the muscle, which is the responsible factor in producing the different degrees of articular inclination I have considered. In 1914 H. Virchow compared the multifidus in quadrupedal Mammals and in Man and suggested that the narrower muscle in the former can act with greater effect on the articular processes and so produce the extremely hypersthenic type characteristic of these animals. If it can do this, is it preposterous to suggest that it is the means by which the infant's column, with its average articular index of 99, is changed into such a hypersthenic one as shown in No. 43, Plate III, with its average index of 35? It may be said that I have shown already that the markedly hypersthenic type of articulation is found more often in women than in men and that one does not commonly associate a greater muscular efficiency with the former sex. To this I would reply by suggesting that to women with their pronounced lordosis and with the possibility of pregnancy a comparatively rigid lumbar column must be of more import than it is to men, while lumbar joints, inadequately hypersthenic, may be a factor in producing the backache so often attributed to insufficient muscular development. Although I recognise that I am making muscular action responsible for a great deal, my conclusion would be, then, that the multifidus is the agent which produces both the change from the

infant to the adult condition and the normal difference between the upper and the lower lumbar articular facets, while by its variable action and development it may cast the whole of the lumbar and the lumbo-sacral diarthrodial joints into one of the three categories into which they have been divided in this paper.

SUMMARY

1. The index of articular inclination was determined in the disarticulated lumbar column and sacrum from a mixed lot of 44 skeletons, 26 male and 18 female. This was supplemented by small series of the same measurements of similar bones from children, some primitive races and anthropoids.

2. While it is subject to considerable variation in individual columns, the average formula of the order of inclination of the articular processes for the lumbar vertebrae and sacrum in either sex is L 1 < L 2 > L 3 > L 4 > L 5 > S.

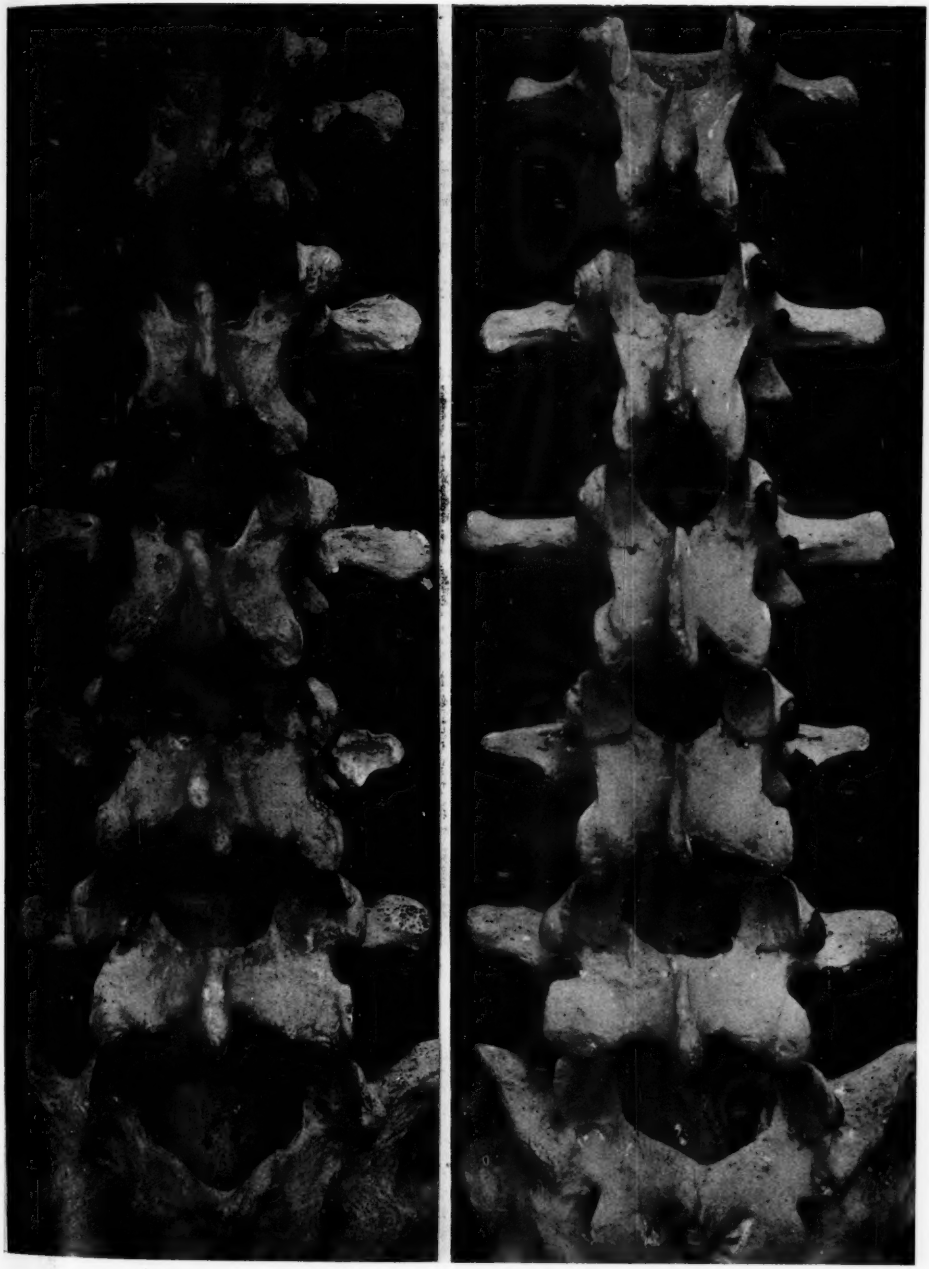
3. Both columns and sacra fall into three groups according to the average degree of the inward inclination of their articular facets. These groups are here termed hypersthenic, average and asthenic. The hypersthenic type occurs more frequently in female lumbar columns, the asthenic in male. There is the same tendency in the lumbo-sacral joints, but it is much less marked.

4. The lumbar and lumbo-sacral joints are alike in type in one-third of this series, while in the other two-thirds the lumbar articulations correct the lumbo-sacral joint by making the combined average of them all more hypersthenic in half and more asthenic in the rest.

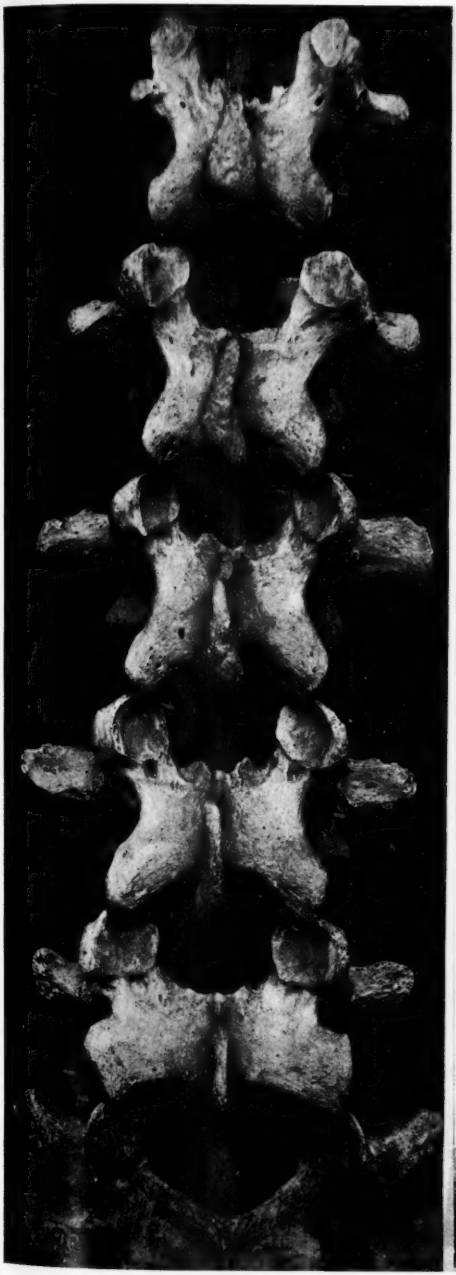
5. There is not usually any abrupt change in the direction of the facets at the lumbo-sacral junction. The superior articular processes begin to open out at the 3rd lumbar and in the vertebrae below this the trend of the articular surfaces is increasingly towards the frontal plane. Here there must be in many cases potential rotatory movement.

6. The differences seen in the degree of inclination of the articular facets are due, it is suggested, to the variable development and action of the multifidus spinae muscle.

I wish to express my indebtedness to Prof. Arthur Thomson for much helpful advice, to Dr Dudley Buxton for his great assistance in inventing the method of measurement used in this paper, and to Sir Arthur Keith and Prof. Goodrich for giving me many facilities at the Royal College of Surgeons and in the Department of Comparative Anatomy at Oxford respectively. Also I must thank Mr W. Chesterman, of this Department, and Mr H. George, of the Royal College of Surgeons Museum, very much for the production of these photographs, and Messrs Rouilly and Co. for the loan of several vertebral columns.

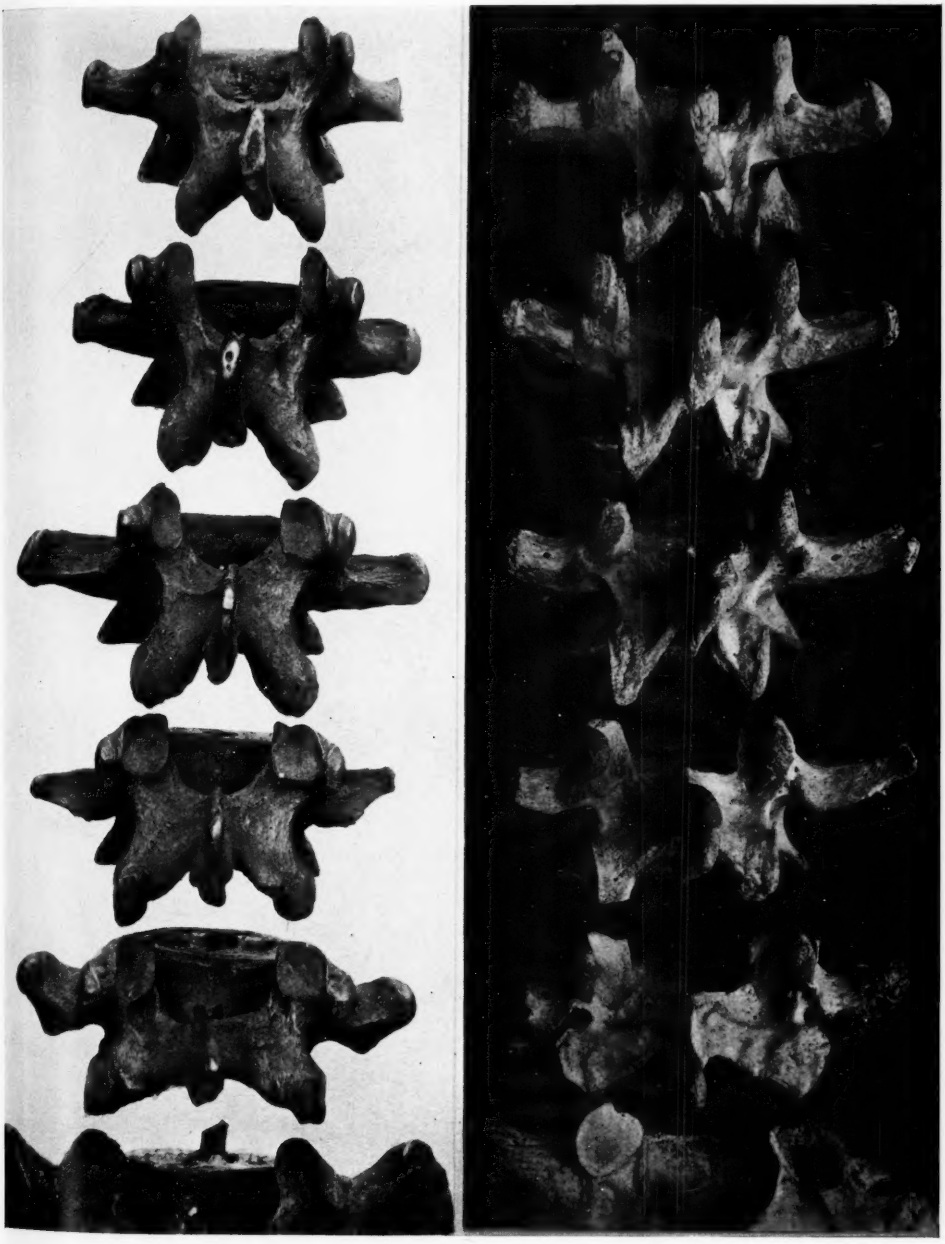


No. 7. No. 39.



No. 18.

No. 25.



No. 32. No. 43.

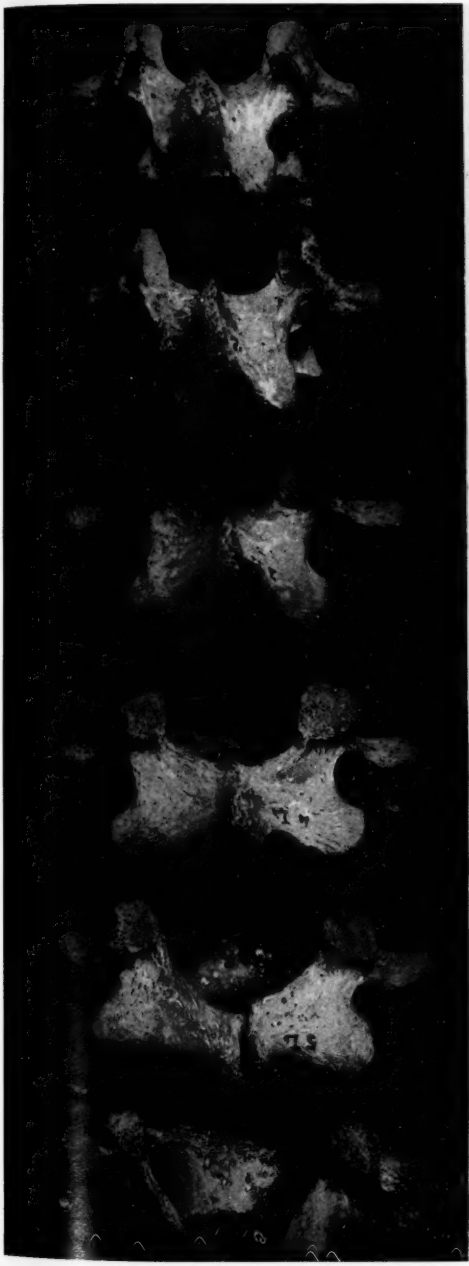


Fig. 1.

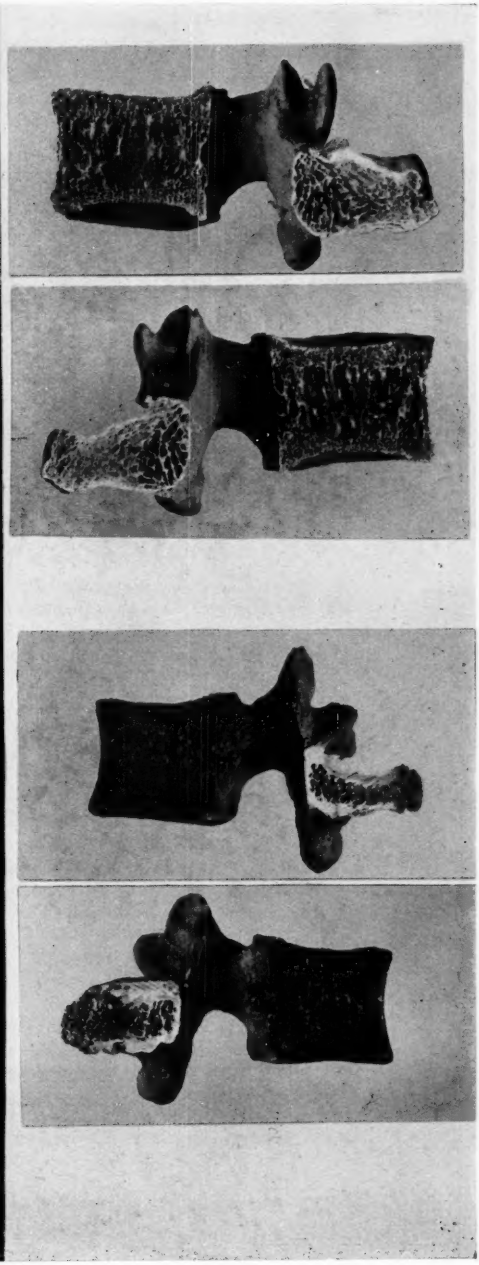


Fig. 2.

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EXPLANATION OF PLATES

PLATE I

These are both photographs of average columns and sacra. No. 7 is from a male and has an average articular index of 61 for the lumbar joints, while that of the lumbo-sacral joint is 72: combined average index 63. No. 39 is from a female and has corresponding averages of 55 for the lumbar joints and 85 for the lumbo-sacral: combined average index 60.

PLATE II

Here two male columns are contrasted. No. 18 is of the asthenic type throughout with an average index of 76 for the lumbar joints and with an index of 85 for the lumbo-sacral articulation, giving a combined average of 78. In No. 25 the column is hypersthenic with an index of 43 and compensates for the asthenic and arthritic lumbo-sacral joint with an index of 95, making the combined index 54.

PLATE III

Two female columns are compared. No. 32 is asthenic with an average index of 64 for the lumbar joints: the sacral articular index is 71 and the combined average is 66. No. 43 is the most hypersthenic column I have measured with an average index of 35. This compensates for a lumbo-sacral joint with an index of 88 and the combined average is 44.

PLATE IV

Fig. 1 is a photograph of the lumbar vertebrae and the first piece of the sacrum from a boy of 8 years old. The average index for the column is 83, for the sacrum 94.

Fig. 2 shows two 12th dorsal vertebrae, divided in the mid-line, with unilateral lumbarisation of the superior articular facets. The upper photograph comes from a modern column, the lower is a Romano-British vertebra. In the 2nd and 4th photographs the ossification of the superior tubercle of the transverse process involves the lateral border of the articular surface and draws it backwards. In the 1st and 3rd this has not occurred and the articular surface remains dorsal in type.

CRANIOMETRIC MEMOIRS

No. V. THE INFERIOR GNATHIC TRIANGLE. A NEW CRANIAL TRIANGLE. ITS SIGNIFICANCE IN MODERN AND FOSSIL MAN, THE ANTHROPOIDS AND LOWER MAMMALS

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THIS paper is a direct sequel to Craniometric Memoir No. III, which recorded the results of a study of the superior gnathic triangle. The cranial material that was utilised in that research was again made use of for the present investigation.

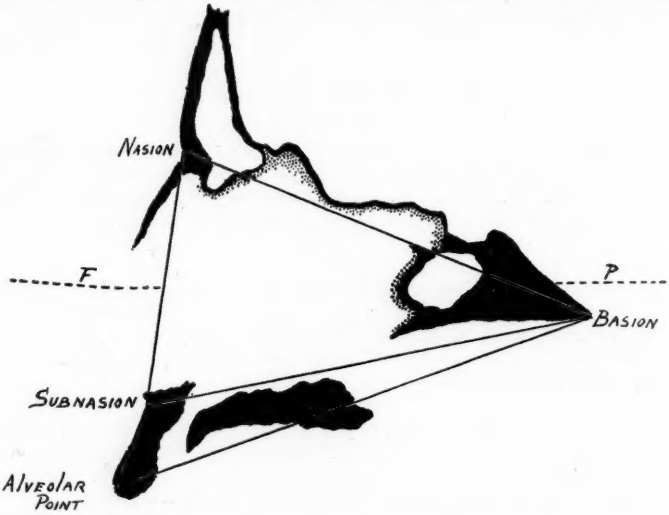

Fig. 1. Part of a mesial section of Hamann Museum male Negro cranium No. 662, to show the superior and inferior gnathic triangles recently devised by the author. Note that the greater part of the prognathism in this skull is produced by the inferior gnathic triangle.

As fig. 1 shows, the salients of the inferior gnathic triangle are situated at the basion, the alveolar point and the subnasion. Its three sides are therefore the basion-subnasion, basion-alveolar and the subnasion-alveolar. Of these the basion-alveolar has been for long a well-recognised cranial dimension. The other two sides of the triangle, namely the basion-subnasion and the subnasion-alveolar dimensions, have never been previously described. They are therefore discussed in separate communications (2,4) which are being published elsewhere.

It is necessary to mention that the author has also made a study of the relative proportions of the three sides of the triangle in Man and in the lower Mammals. In this way three new cranial indices have been produced, which were found to possess an unusual degree of significance. They are also to form the subject of a separate communication (5). In the present paper the human and comparative anatomy of the three constituent angles of the inferior gnathic triangle will be dealt with. They will, for the sake of brevity, be referred to in this paper as the S.-A.-B., A.-S.-B. and S.-B.-A. angles, where S. represents the subnasion, B. the basion and A. the alveolar point. This paper is to be regarded as of the nature of a preliminary communication.

I. THE S.-A.-B. ANGLE OF THE INFERIOR GNATHIC TRIANGLE

The salient of the S.-A.-B. angle of the inferior gnathic triangle is situated at the alveolar point (fig. 1). It was found to exhibit wide ranges of variation in both the White and the Negro crania of the Hamann Museum.

Table I. *The S.-A.-B. angle of the inferior gnathic triangle exhibited very wide ranges of variation in the Hamann Museum White and Negro crania.*

	Maximum	Minimum	Range of variation
Hamann Museum male White	94·2°	63·1°	31·1°
Hamann Museum female White	78·3°	58·3°	20°
Hamann Museum male Negro	80·5°	55·2°	25·3°
Hamann Museum female Negro	76·6°	47°	29·6°

The standard deviations for the male Whites, male Negroes, female Whites and female Negroes were 5·11, 4·94, 5·18 and 5·01. The coefficients of variation were 6·46, 7·71, 7·11 and 8.15 respectively.

The average size of the S.-A.-B. angle of the inferior gnathic triangle

The average size of this angle in the Hamann Museum male White crania was found to be 79·6°. That is to say, it approached a right angle. The average dimension for the male Negro crania proved to be decidedly less, namely 64·3°. An examination of fig. 1 will show that this angle would naturally tend to become very much reduced in size in the more prognathic type of skull. This racial difference was of course amply confirmed by a study of the female crania. Thus the angle presented an average dimension of 72·8° in the female White crania, whereas in the female Negro crania the corresponding dimension was only 61·4°. A further study of these Negro crania disclosed the fact that, though both their superior and inferior gnathic triangles were affected by prognathism, the inferior triangle was much more involved in this condition than the superior.

The results for these Hamann Museum crania have been tabulated in Table II, an inspection of which will show that there was evidently a sexual as well as a racial factor determining the size of the S.-A.-B. angle. The latter, it may be noted, exhibited a lower average dimension in the females than in the males of both races, thus suggesting that the female crania were on the average

slightly more prognathic than the male crania. The fact that this reduction was exhibited by the females of two very diverse racial groups, appeared to impart to it some degree of significance. Indeed, these observations afforded ample confirmation of the author's previous researches on the influence of the sexual factor upon the gnathic index (1). Thus he found that the latter index was, in the case of the Hamann Museum White and Negro crania higher on the average in the females than in the males. That is to say, this index showed that the females were on the average slightly more prognathic than the males in both these racial groups.

Table II. *The average size of the S.-A.-B. angle of the inferior gnathic triangle was less in the Hamann Museum Negro than in the Hamann Museum White, and also less in the females than in the males of both races, thus suggesting the existence of a sexual as well as a racial factor.*

	Males	Females
Hamann Museum White	79·6° ± 0·4449	72·8° ± 0·45107
Hamann Museum Negro	64·3° ± 0·4301	61·4° ± 0·4362

The author's next course was to study the S.-A.-B. angle in the male Eskimo crania. The average dimension for this racial group proved to be 70·3°, which was definitely lower than the average for the Hamann Museum male White. In Craniometric Memoir No. III the author showed that the superior gnathic triangle in these Eskimo crania exhibited a slight degree of prognathism when compared with the male White crania. The results of the present investigation so far tended to show that these Eskimo crania displayed a slight prognathic condition in the case of their inferior gnathic triangles as well. Further, a comparison of both triangles in this Eskimo group showed that the inferior gnathic triangle was more affected by prognathism than the superior triangle.

The average dimension of the S.-A.-B. angle in the male Mongol crania was found to be 68·3°, that is to say, lower than the average for the male Eskimo crania. The information thus obtained showed that the inferior gnathic triangle in this Mongol cranial group was on the average more prognathic than in the White and the Eskimo crania. The author showed in Craniometric Memoir No. III that the superior gnathic triangle in these Mongol crania was remarkably orthognathic. Therefore the prognathism in this racial group appeared to be confined solely to the inferior gnathic triangle.

The native Australian crania provided an average S.-A.-B. angle of 66·1°, which was slightly higher than that for the male Negroes, instead of lower, as one would have expected in the more lowly evolved racial type. As only five Australian crania were available for study, future investigation will probably show that the racial average was lower than this. This impression was in a measure confirmed by the fact that a prognathic male Melanesian skull (3) yielded a S.-A.-B. angle as low as 54·2°.

The crania that were available to represent fossil Man provided some

instructive results. As the various measurements were made on casts of the original crania, they will have to be taken as approximate. The original crania, except the Rhodesian, were not accessible. The Combe Capelle skull yielded a S.-A.-B. angle of 76·6°, which closely approached the average for the male White crania. This signified that the inferior gnathic triangle in this specimen was remarkably orthognathic, and thus conformed to the European type. As was to be expected, this angle exhibited a smaller dimension in the La Chapelle skull, namely 72·8°, though it was well above the average for the Negro crania. Thus the information yielded by a study of the two gnathic triangles of this prognathic skull indicated that its prognathism was produced much more by the superior than by the inferior triangle. On the other hand, the Rhodesian skull provided a S.-A.-B. angle of only 58·9°, which suggested a marked degree of prognathism affecting its inferior gnathic triangle. The writer has shown in Craniometric Memoir No. III, that the superior gnathic triangle of this skull was only slightly affected by prognathism. The La Chapelle and Rhodesian skulls thus provided a marked contrast to one another with reference to the relative degree of prognathism affecting their gnathic triangles.

The results of this comparative study of the S.-A.-B. angle in modern and fossil Man are displayed in Table III. The author has inserted the gnathic indices for these crania in the same table, for the purpose of showing that this angle diminishes, while the gnathic index increases, with progressive degrees of prognathism. It must be clearly understood, however, that the S.-A.-B. angle is an index of prognathism involving only the inferior gnathic triangle, whereas the gnathic index is an index of prognathism involving the whole gnathic triangle. The gnathic indices given for fossil Man in Table III must be accepted as approximate, as they had to be calculated from measurements made upon casts. The index for the Rhodesian skull was taken from Pycraft's memoir (6).

Table III. *The S.-A.-B. angle of the inferior gnathic triangle diminishes, while the gnathic index increases, with progressive degrees of prognathism.*

	S.-A.-B. angle	Gnathic index
Male White (Hamann Museum)	79·6°	92·9
Male Eskimo (U.S.N. Museum)	70·3°	97·6
Male Mongol (U.S.N. Museum)	68·3°	95·4
Native Australian (U.S.N. Museum)	66·1°	100·6
Male Negro (Hamann Museum)	64·3°	100·8
Combe Capelle skull (approx.)	76·6°	96·8
La Chapelle skull (approx.)	72·8°	105·9
Rhodesian skull (approx.)	58·9°	105

Comparative anatomy of the S.-A.-B. angle of the inferior gnathic triangle

The information provided by a study of this angle in modern and fossil Man, showed very definitely that it attained its maximum dimensions in the orthognathic skull of the White races. As a natural sequel, it was found to exhibit a definite reduction in the prognathic crania of the lower races of mankind. As a natural result of these observations, one would expect the S.-A.-B.

angle to continue to display this progressive diminution in its dimensions as one descended the mammalian series. This diminution, as it transpired, was found to be most pronounced. For example, one of the highest anthropoids, namely the gorilla (B 170 of the Hamann Museum), presented a S.-A.-B. angle of only 36·9°, which represented a reduction of more than half, when compared with the average dimension for the White races. The other two highest anthropoids made a better showing. Thus the skull of a chimpanzee (B 240 of the Hamann Museum) furnished an angle of 48·2°, and that of an orang (B 551of the Hamann Museum) an angle of 67·2°. The skull of a gibbon (B 549 of the Hamann Museum) exhibited a S.-A.-B. angle of 58·3°. It was thus possible that in the anthropoids this angle displayed the usual wide ranges of variation as in Man. When large collections of crania representing these genera are available, so as to permit of an average being taken, it will be found that a perceptible evolutionary gap exists between the Hominidae and the anthropoids.

Table IV. *The S.-A.-B. angle of the inferior gnathic triangle exhibits a progressive diminution in size, as one descends the mammalian series, until it finally becomes reduced to zero.*

Male White (Hamann Museum)	79·6°
Male Negro (Hamann Museum)	64·3°
Native Australian (U.S.N. Museum)	66·1°
Rhodesian skull (approx.)	58·9°
Chimpanzee	48·2°
Gorilla	36·9°
Orang	67·2°
Gibbon	58·3°
Pithecus	31·5°
Tarsius	Nearly zero
Dog	Nearly zero
Lemur	Zero

The lower anthropoids were represented by the skull of a macaque monkey (B 416 of the Hamann Museum). This possessed a S.-A.-B. angle of only 31·5°, which showed a further reduction, when contrasted with the higher anthropoids.

It was found that the S.-A.-B. angle was undergoing a somewhat dramatic change in the Lemuroidea, for it was evidently in process of obliteration in this Primate group. This meant of course that the whole inferior gnathic triangle was being literally wiped out. The skull of *Lemur catta* (B 197 of the Hamann Museum) that was available for this investigation was of course very small. A minute examination, however, showed that the subnasion and alveolar point had become so closely approximated as to be no longer recognisable as separate craniometric points. There were thus no means of estimating the dimensions of the three angles of the inferior gnathic triangle in this specimen. All that one could surmise, however, was that the A.-S.-B. angle had practically attained to 180°, while the other two angles had become reduced to zero. The skull of *Tarsius* (B 135 of the Hamann Museum) was excessively small. The author, however, thanks to the kindness of Prof. Wingate Todd, was enabled to study a photograph of a mesial section of this skull magnified five times. This photo-

graph certainly suggested that the inferior gnathic triangle was much more in evidence in this skull than in the case of the skull of *Lemur catta* (compare figs. 2 and 3). The skull of a dog (B 128 of the Hamann Museum) exhibited practically the same condition as that shown by the Lemuroidea. That is to say, the inferior gnathic triangle was in process of obliteration in this specimen. We thus obtained most valuable information to the effect that in lower Mammals below the level of the anthropoids the prognathism of their crania was almost entirely produced by the superior gnathic triangle, whereas in the Hominidae the most important type of prognathism was that involving the inferior gnathic triangle.

II. THE A.-S.-B. ANGLE OF THE INFERIOR GNATHIC TRIANGLE

The salient of the A.-S.-B. angle of the inferior gnathic triangle is situated at the subnasion (fig. 1). It displayed extensive ranges of variation in the Hamann Museum White and Negro crania.

Table V. *The ranges of variation of the A.-S.-B. angle of the inferior gnathic triangle in the Hamann Museum White and Negro crania.*

	Maximum	Minimum	Range of variation
Hamann Museum male White	107·9°	73·8°	34·1°
Hamann Museum female White	103·6°	83·3°	20·3°
Hamann Museum male Negro	115·2°	88·5°	26·7°
Hamann Museum female Negro	124·5°	92·5°	32°

The standard deviations for the male Whites, male Negroes, female Whites and female Negroes were 5·15, 4·81, 4·98 and 4·84. The coefficients of variation were 5·69, 4·58, 5·14 and 4·48 respectively.

The average size of the A.-S.-B. angle of the inferior gnathic triangle

The average dimension of this angle in the Hamann Museum male White crania was found to be 90·5°, that is to say, practically a right angle. The male Negro crania provided a marked contrast to this by furnishing an average dimension of as much as 105·9°. It was thus evident that this angle became markedly increased in size in the prognathic crania of the lower Hominidae, as fig. 1 shows. These observations were confirmed by an examination of the Hamann Museum female crania. Thus the average dimension of the A.-S.-B. angle in the female White crania was 96·8°, as against 108·8° for the female Negroes.

These results are recorded in Table VI, from which it will be noted that there were definite evidences of a sexual factor as well as a racial factor, determining the size of this angle. Thus it will be observed that the average size of the A.-S.-B. angle was greater in the females than in the males in both the White and the Negro crania. These findings confirmed the evidence yielded by the S.-A.-B. angle. They also provided support to the results of the author's observations on the gnathic index (1) which showed that the Hamann Museum female crania, both White and Negro, were slightly more prognathic on the average than the males of these racial groups.

Table VI. *The average size of the A.-S.-B. angle of the inferior gnathic triangle is greater in the Hamann Museum Negro than in the Hamann Museum White, and also greater in the females than in the males of both these racial groups, thus suggesting the existence of a sexual as well as a racial factor.*

	Males	Females
Hamann Museum Negro	105·9° ± 0·4188	108·8° ± 0·4214
Hamann Museum White	90·5° ± 0·4484	96·8° ± 0·4336

The average dimensions of the A.-S.-B. angle of the inferior gnathic triangle in the male Eskimo crania proved to be 100·1°, that is to say, well above the average for the Hamann Museum White crania. This angle thus confirmed the observations made on the S.-A.-B. angle in this racial group, the conclusion being that the inferior gnathic triangle in these Eskimo crania was more prognathic than in the Hamann Museum White crania.

The average dimension of the A.-S.-B. angle in the male Mongol crania was ascertained to be 100·8°, that is to say, closely similar to that for the Eskimo crania. The native Australian crania, on the other hand, displayed the high average of 106·9°, as one would have expected in this lowly evolved racial type. It is of interest to record here that a very prognathic male Melanesian skull (3) furnished an angle as large as 113·2.

Among the types that were available to represent fossil Man it was found that the Combe Capelle skull showed the closest approximation to the European type, with a A.-S.-B. angle of 94·1°. The La Chapelle skull yielded an angle of 99·5°, thus confirming the results shown by the S.-A.-B. angle of this skull, in indicating that its inferior gnathic triangle was less affected by prognathism than its superior gnathic triangle. On the other hand, the Rhodesian skull provided a A.-S.-B. angle of 106·5°, thus suggesting that the inferior gnathic triangle of this skull showed a greater tendency to prognathism than its superior gnathic triangle.

The results yielded by this study of the A.-S.-B. angle of the inferior gnathic triangle are displayed in Table VII. The corresponding gnathic indices have

Table VII. *The gnathic index and the dimensions of the A.-S.-B. angle of the inferior gnathic triangle follow one another more or less consistently. That is to say, both increase with progressive degrees of prognathism.*

	A.-S.-B.	Gnathic index
Male White (Hamann Museum)	90·5°	92·9
Male Eskimo (U.S.N. Museum)	100·1°	97·6
Male Mongol (U.S.N. Museum)	100·8°	95·4
Male Negro (Hamann Museum)	105·9°	100·8
Native Australian (U.S.N. Museum)	106·9°	100·6
Combe Capelle skull (approx.)	94·1°	96·8
La Chapelle skull (approx.)	99·5°	105·9
Rhodesian skull (approx.)	106·5°	105

been inserted in the same table for the purpose of demonstrating that the gnathic index and the dimensions of the A.-S.-B. angle follow one another more or less consistently. That is to say, both increase with progressive degrees of

prognathism. It should be clearly understood, however, that the A.-S.-B. angle is an index of prognathism affecting only the inferior gnathic triangle, whereas the gnathic index is an index of prognathism involving the whole gnathic triangle.

Comparative anatomy of the A.-S.-B. angle of the inferior gnathic triangle

The information yielded from a study of this angle in modern and fossil Man indicated that it was an index of the degree of prognathism involving the inferior gnathic triangle. That is to say, the angle increased in size with progressive degrees of prognathism. It was therefore to be expected that this increase in the dimensions of the A.-S.-B. angle would be displayed to the full in the prognathic crania of lower mammalian types. It was decided to study the angle in the highest anthropoids first of all. The skull of an orang (B 551 of the Hamann Museum) exhibited the nearest approximation

Table VIII. *The A.-S.-B. angle of the inferior gnathic triangle exhibits a progressive increase in size as one descends the mammalian scale, until it finally approximates to* 180°.

Hamann Museum male White	90·5°
Hamann Museum male Negro	105·9°
Native Australian (U.S.N. Museum)	106·9°
Rhodesian skull (approx.)	106·5°
Orang	103·6°
Chimpanzee	122·7°
Gorilla	137·6°
Gibbon	117·5°
Pithecus	144·2°
Lemur	180° (approx.)
Tarsius	180° (approx.)
Dog	180° (approx.)

to the Hominidae, with an angle of 103·6°. It was thus evident that there was no definite evolutionary gap between the Hominidae and the Simiidae, just as in the case of the S.-A.-B. angle. The skull of a chimpanzee (B 240 of the Hamann Museum) furnished an angle much greater, namely 122·7°, while in the skull of a gorilla (B 170 of the Hamann Museum) it was even greater, namely 137·6°. It was of interest to record the fact that the skull of a gibbon (B 549 of the Hamann Museum) recorded an angle of only 117·5°. An enormous increase in the size of the angle, namely to 144·2°, was manifested by the skull of a macaque monkey (B 416 of the Hamann Museum) which was available to represent the lower anthropoids. It was thus evident that the A.-S.-B. angle was rapidly approaching 180°, as one descended the mammalian scale. Indeed this was the condition found in the skull of *Lemur catta* (B 197 of the Hamann Museum), which of course meant the termination of the existence of the inferior gnathic triangle in this genus. As already mentioned in the case of the S.-A.-B. angle, this lemur skull and that of *Tarsius* were so small, that it was hard to differentiate with certainty between the subnasion and the alveolar points as

they were so closely approximated. The skull of a dog showed practically the same condition, so that in these three mammalian types it was evident that the inferior gnathic triangle was being obliterated by the rapid expansion of the superior gnathic triangle (see figs. 2 and 3).

III. THE S.-B.-A. ANGLE OF THE INFERIOR GNATHIC TRIANGLE

The salient of the S.-B.-A. angle is situated at the basion. It is by far the smallest of the three constituent angles of the inferior gnathic triangle. It exhibited very slight ranges of variation in the Hamann Museum White and Negro crania.

Table IX. *The ranges of variation of the S.-B.-A. angle of the inferior gnathic triangle in the Hamann Museum White and Negro crania.*

	Maximum	Minimum	Range of variation
Hamann Museum male White	10·9°	9·1°	1·8°
Hamann Museum female White	9·3°	8·6°	0·7°
Hamann Museum male Negro	10·7°	9·5°	1·2°
Hamann Museum female Negro	10·6°	8·5°	2·1°

The standard deviations for the male Whites, male Negroes, female Whites and female Negroes were 1·50, 1·37, 1·45 and 1·32. The coefficients of variation were 14·28, 13·98, 14·07 and 13·06 respectively.

The average size of the S.-B.-A. angle of the inferior gnathic triangle

The average dimensions of this angle in the Hamann Museum male White crania proved to be 10°. In the male Negro crania, on the other hand, the average size was fractionally less, the exact figure being 9·8°. The racial difference was thus almost negligible, but one had to recollect that in the first place, this cranial angle was extremely small, and secondly, it had very small ranges of variation, as Table IX shows. This racial difference was, moreover, confirmed by the Hamann Museum female crania. Thus the average for the female Whites was 10·3°, as contrasted with 10·1° for the female Negroes, that is to say, the angle was again slightly smaller on the average in the Negro type of skull.

It was rather interesting to note that this angle, like the other two constituent angles of the inferior gnathic triangle, suggested the existence of a sexual as well as a racial factor. Thus it will be observed from Table X that it was fractionally larger in the females than in the males of both racial groups. It is true that this sexual difference was merely fractional, but it had to be remembered that one was dealing with a very tiny angle. However, the fact that this sexual difference was consistently displayed by both the White and the Negro crania appeared to confer upon it some degree of significance.

Table X. *The S.-B.-A. angle is on the average fractionally smaller in the Hamann Museum Negro than in the Hamann Museum White. It is also larger in the females than in the males of both races, thus suggesting the existence of a sexual as well as a racial factor.*

	Males	Females
Hamann Museum White	10° ± 0·1306	10·3° ± 0·1262
Hamann Museum Negro	9·8° ± 0·1192	10·1° ± 0·1149

The average dimensions of the S.-B.-A. angle in other racial types of modern Man presented no special features. The average for the male Eskimo crania was 9·1° and for the male Mongol crania 10·9°. The high figure yielded by the latter was explainable in great measure by the unusual subnasion-alveolar height displayed by these crania (4). The average size of the S.-B.-A. angle in the native Australian crania was unusually low, namely 6·9°.

On coming to the types representing fossil Man, it was noted that the Rhodesian skull yielded a S.-B.-A. angle of 14·7°, which was far beyond the maximum dimensions for modern Man given in Table IX. This was explained by an excessive subnasion-alveolar height which, as the writer has recently shown (4), was quite a feature of this skull. In contrast to this, the S.-B.-A. angle for the La Chapelle skull was only 7·5°, which was of course below the minimum dimension for modern Man. The Combe Capelle skull yielded an angle of 9·6°, which was well within the range of variation for modern Man.

Comparative anatomy of the S.-B.-A. angle of the inferior gnathic triangle

The skull of a chimpanzee (B 240 of the Hamann Museum) yielded a S.-B.-A. angle of 9·1°, which, as it happened, was also the dimension shown by the skull of an orang (B 551 of the Hamann Museum). These were of course within the range of variation for modern Man. The angle furnished by a gorilla skull (B 170 of the Hamann Museum) was much smaller, namely 5·1°. This reduction was continued in the gibbon skull (B 549 of the Hamann Museum), the angle in this case being only 4·8°. It was in the lower anthropoids, however, that the angle showed its most marked shrinkage. For instance, the skull of a macaque monkey (B 416 of the Hamann Museum) presented a S.-B.-A. angle of only 2·8°. It was thus clear that this angle was in process of obliteration, and with it of course the inferior gnathic triangle. This was confirmed by a study of the Lemuroidea (*Tarsius* and *Lemur catta*) and the skull of a dog, in none of which could the angle be estimated with any degree of satisfaction. In these three genera, therefore, the angle was clearly approximating to zero.

Table XI. *The S.-A.-B. and the S.-B.-A. angles of the inferior gnathic triangle gradually diminish in size as one descends the mammalian scale, until they finally approximate to zero. On the other hand, the A.-S.-B. angle gradually increases, until it finally approximates to* 180°.

	S.-A.-B. angle	A.-S.-B. angle	S.-B.-A. angle
Male White (Hamann Museum)	79·6°	90·5°	10°
Male Negro (Hamann Museum)	64·3°	105·9°	9·8°
Native Australian (U.S.N.M.)	66·1°	106·9°	6·9°
Chimpanzee	48·2°	122·7°	9·1°
Gorilla	36·9°	137·6°	5·1°
Orang	67·2°	103·6°	9·1°
Gibbon	58·3°	117·5°	4·8°
Pithecus	31·5°	144·2°	2·8°
Tarsius	Nearly zero	180° (approx.)	Nearly zero
Dog	Nearly zero	180° (approx.)	Nearly zero
Lemur	Zero	180° (approx.)	Zero

GENERAL DISCUSSION OF ALL THREE ANGLES OF THE INFERIOR GNATHIC TRIANGLE AND OF THE TWO GNATHIC TRIANGLES IN GENERAL

In the first place, one must refer to the outstanding result of this investigation, namely, that the inferior gnathic triangle becomes profoundly affected by prognathism, particularly in the lower Mammalia. For instance, it was noted that the S.-A.-B. and the S.-B.-A. angles diminished in size, as one descended the mammalian scale, until finally they both became reduced to zero. On the other hand, the A.-S.-B. angle underwent a rapid increase in size in the lower Mammalia until it finally reached 180°. All these facts meant, of course, that the inferior gnathic triangle was being gradually obliterated, as one descended the mammalian series, until it finally disappeared (e.g. in *Lemur catta*). This observation alone was sufficient to warrant the creation by the author of his superior and inferior gnathic triangles.

It is therefore important and likewise opportune to make a brief survey of the relative amounts which these two triangles contribute to the prognathism of Man and lower Mammals. The superior gnathic triangle was orthognathic in the White crania, both male and female, and comparatively so in the Mongolian races, i.e. the Eskimo and the Mongol. It exhibited a slight degree of prognathism in the Black races, as represented by the Hamann Museum Negro, the native Australian and the Melanesian. In the crania representative of fossil Man this triangle exhibited a marked degree of prognathism in the La Chapelle specimen and slighter evidences of this condition in the Rhodesian skull. In comparison with these, the Combe Capelle skull was relatively orthognathic. In the anthropoids it was ascertained that the superior gnathic triangle had become markedly prognathic, when compared with the condition found in Man, but no marked difference was displayed by the higher and the lower members of that group. In the Lemuroidea, however, as typified by *Lemur catta*, the whole of the prognathism was found to be that produced by the superior gnathic triangle, owing to the fact that the inferior gnathic triangle had become obliterated in that genus.

The inferior gnathic triangle was definitely orthognathic in the male White crania, but less so in the females of that cranial group. It was thus evident that a sexual factor existed in the case of this triangle. Indeed, this observation confirmed the author's previous researches (1) regarding the influence of a sexual factor upon the gnathic index. The inferior gnathic triangle was less orthognathic in the Mongolian races (Eskimo and Mongol) than in the White races. It was noted that in the Black races, as represented by the Hamann Museum Negro, the Melanesian and the native Australian, the inferior gnathic triangle contributed far more to their prognathism than did the superior gnathic triangle. Moreover, it was observed that in the Hamann Museum female Negro the inferior gnathic triangle was more prognathic than in the males of that cranial group, thus suggesting the existence of a sexual factor in this case, just as was found in the White crania.

In the crania of fossil Man it was found that in the Combe Capelle specimen both the superior and inferior gnathic triangles conformed to the European orthognathic type. In the Rhodesian skull the inferior gnathic triangle displayed much more prognathism than the superior triangle. On the other hand,

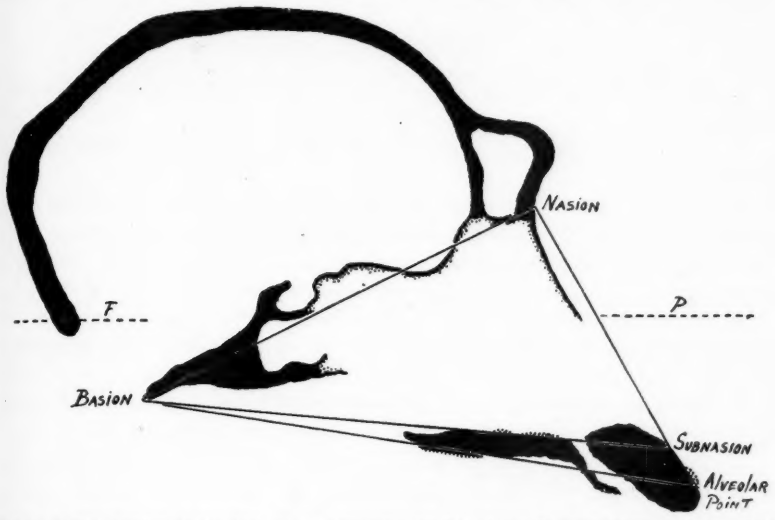

Fig. 2. Mesial section of the skull of a chimpanzee (B 240 of the Hamann Museum). It will be noted that the superior gnathic triangle contributed far more to the prognathism of this skull than its inferior gnathic triangle. The latter is showing the first signs of its suppression, produced by the gradual approximation of the subnasion and the alveolar point.

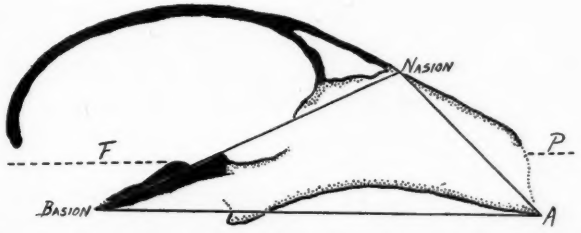

Fig. 3. Mesial section of the skull of a lemur (B 197 of the Hamann Museum), showing the final stage of approximation of the subnasion and the alveolar point (at *A*), thus causing the obliteration of the inferior gnathic triangle. The prognathism in this skull is therefore created entirely by its superior gnathic triangle.

the major portion of the prognathism in the very prognathic La Chapelle skull was found to be produced by the superior gnathic triangle.

The comparative anatomy of the inferior gnathic triangle proved an interesting study. In the highest anthropoids it was found to contribute in a

considerable degree to the prognathism of their crania. In the lower anthropoids, on the other hand, it came to occupy a subsidiary position in this respect, the last phase of all being its complete obliteration in lower mammalian types, as already mentioned.

CONCLUSIONS

1. The inferior gnathic triangle is a new cranial triangle recently devised by the author.

2. Its three constituent angles are described for the first time in this paper.

3. The salients of the triangle are at the basion, alveolar point and subnasion, the last being a new craniometric point devised by the author. The three angles are therefore the subnasion-alveolar-basion (S.-A.-B.), the alveolar-subnasion-basion (A.-S.-B.) and the subnasion-basion-alveolar (S.-B.-A.).

4. All three angles were definitely affected by prognathism. They all exhibited alterations in their dimensions in the Black races, when compared with the White races.

5. All three angles displayed the existence of a sexual as well as a racial factor in the case of the Hamann Museum White and Negro crania.

6. The dimensions of all three angles became profoundly affected by the prognathism of lower Mammals. For example, the S.-A.-B. and S.-B.-A. angles diminished as one descended the mammalian scale, until they finally approximated to zero in the Lemuroidea. On the other hand, the A.-S.-B. angle rapidly increased as one descended the mammalian scale, until it finally approximated to 180° in the Lemuroidea. That is to say, the inferior gnathic triangle tended to disappear altogether.

7. In the Rhodesian skull the inferior gnathic triangle displayed much more prognathism than its superior gnathic triangle. On the other hand, the major portion of the prognathism of the very prognathic La Chapelle skull (cast) was found to be produced by its superior gnathic triangle.

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THE ANATOMY OF A DOUBLE-HEADED SNAKE

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INTRODUCTION

Recent advances in experimental embryology have indicated that abnormal embryos may be induced to develop from normal eggs by any of a number of external conditions. While investigation of teratological phenomena may provide valuable clues for understanding normal processes there is a striking difference between the products of experimental embryology and the naturally occurring teratological specimens. The former do not appear to be capable of reaching a post-embryonic condition even under the favourable conditions possible in a laboratory, while examples of the latter category which have been recorded have usually reached this later stage and in a few instances have been sufficiently well adjusted to their environment to become mature. It is possible that this difference between artificially produced and naturally occurring specimens is due to selection from a much larger number of unobserved naturally occurring abnormal forms, but we are nevertheless faced with the problem of how individuals with unusual organisations are readjusted so that they will function under natural conditions. This is but part of the larger problem of adaptation, and before dealing with the problem of how this readjustment is brought about we do well to enquire what modifications are to be found in successful abnormal individuals. Snakes, with their lack of lateral appendages, provide relatively simple teratological examples, especially of double monsters, and as they do not occur frequently it is advisable to place on record whatever information can be obtained to facilitate comparison with any which may be produced under artificial conditions.

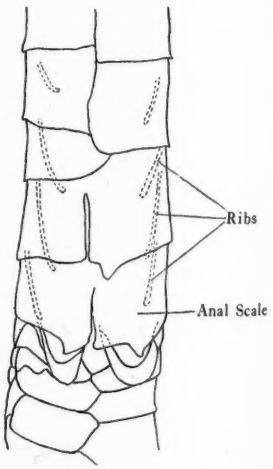
Altogether since records have been kept, some seventy cases of double-headed snakes have been described, of which only seven have been dissected (Redi, 1684; Vsevolojsky, 1812; Dutrochet, 1829; Dorner, 1873; Borgert, 1896; Cantoni, 1921; Strohl, 1925). As long ago as 1684 Redi made as detailed an examination as has yet been recorded, and the much more recent paper by Strohl gives no more information about his new specimen than that the creature possessed two hearts, one more anterior than the other exhibiting situs inversus.

MATERIAL

The present account is of a male double-headed specimen of *Coluber* (*Zamenis*) *florulentus* Schlegel, University Museum of Zoology, Cambridge, No. R 12960. It had been captured at Cairo and preserved in alcohol. The adult of this species reaches a length of just over 1 m. The total length of the preserved specimen was 25 cm., it was therefore probably quite young.

External features.

No significant difference could be detected in the length or breadth of the two heads, but whilst one head undoubtedly followed the axis of the body the other projected at about 25° to the right of this axis and was rotated on the vertebral column until the angle between the ventral surfaces of the two heads was about 120°. That this was not an accident of fixation is indicated by the relationship of the vertebrae. The mouths and oesophagi of both sides appeared to be equally capable of functioning.



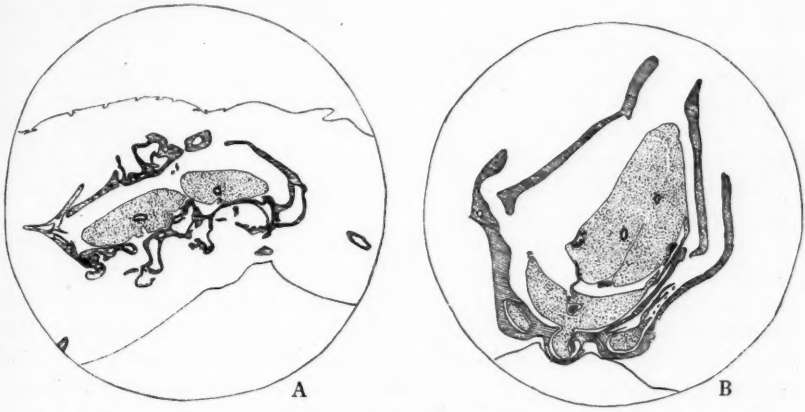
Text-fig. 1. Ventral view of the anal scaling showing the ribs as seen in a transparent preparation.

At the level of the second neck band, 23 mm. from the tip of each snout, the integument of the two "necks" united to form a common investment. At this point there was a transverse and somewhat stretched fold of skin. Posterior to this fold the two parts were indicated by asymmetrical marking. A ventral groove extended for the whole length of the animal in the middle line, and that this was undoubtedly more than a phenomenon of fixation was shown by the fact that most of the ventral scales had an irregularity which took the form of a posteriorly directed projection to the left of the groove. An enlarged diagram of the anal region shows the slight abnormality of the scaling (text-fig. 1). A Spalteholz transparent preparation showed that the anal scale was attached to two pairs of ribs and that the additional scale was without a rib attachment. At a distance of $2\frac{1}{2}$ cm. behind the fold of integument there was a pronounced

bend in the body axis. The accompanying photographs make further description of the external features unnecessary (see Plate I, figs. 1 and 1*a*).

The axial skeleton and nervous system

An X-ray photograph (Plate I, fig. 2) shows that the bend in the body axis occurred at the junction of the right "neck" with that of the main axis. The bend half-way along the right vertebral column took place where doubling was externally apparent and marked the point at which the right "neck" could move independently of the left. Counting from the common vertebrae to this point, it was possible to identify corresponding vertebrae in the two columns; in front correspondence failed as the left column was made up of twenty-four and the right of twenty-five vertebrae. The junction between the two columns extended over four vertebrae.



Text-fig. 2. Transverse sections of vertebrae close to the confluence of the two "necks." Nerve tissue stippled. Skeletal tissue cross hatched.

Serial sections of this region show that on passing backwards the approaching walls of the vertebrae first fused and then disappeared, leaving two separate spinal cords within one vertebra. The sagittal planes of these two cords were then inclined at rather less than 30°. The right cord appeared to bend slightly towards the left and the two came into contact, the right cord slightly ventral to the left. Further backwards the central canals of the spinal cords moved towards one another, the left remaining dorsal to the right. Finally the right central canal turned upwards and ran into the left canal (text-fig. 2 *a*). Fusion of the two spinal cords occurred along a line drawn from the dorsal side running backwards and downwards through the central canals to the ventral side. Ventral to this line two spinal cords could be distinguished, dorsal to it a normal single spinal cord.

A pair of abnormal ventral roots arose where the two spinal cords were closely applied to each other but anterior to the confluence of the two central

canals. Before passing out from the vertebral canal these roots ran into a large mass of nerve tissue which connected the two sides (text-fig. 2 *b*). From this ganglion the nerves ran backwards and outwards through the vertebra to supply the dorsal musculature.

The alimentary system

The jaws, mouths and alimentary canals of both sides were equally well developed and capable of functioning. Measurement of the diameters of the oesophagi in serial sections showed some variation along the length of each, but on the whole the right was slightly smaller than the left. Fusion of the dorsal mesentery 3 mm. behind the transverse fold of skin formed a transverse mesentery which sloped backwards and downwards and which was drawn out to form a partition between the two oesophagi. The alimentary canals did not join until the pylorus, and there were two stomachs. The muscle layer surrounding the endoderm was thick in this region, and the muscle of the two sides formed a single complete tube surrounding the two glandular tubes. When these inner tubes began to fuse the dividing wall first broke down dorsally, leaving for a short distance a septum projecting from the ventral side. The intestine was normal, and the stage of development was indicated as rather young by the existence of but one intestinal bend whereas in older specimens such bends are numerous.

The pancreas was divided, the right part opened into the intestine about 1 mm. behind the left, just at the point of fusion of the two endodermal tubes, not into either the right or left tubes but into a short anteriorly directed diverticulum of the single duodenum which stretched from the ventral to the dorsal side passing to the left of the canals (text-fig. 3). From each of the two gall bladders ran cystic ducts which, becoming bile ducts, passed through the corresponding pancreas and opened into the intestine. The liver was single, but from it there ran two ducts, a normal one to the right pancreas forming a normal bile duct, the other branched at the level of the gall bladders and ran into each cystic duct half-way between the bladder and the pancreas (text-fig. 4). Closely applied to the anterior end of the right pancreas was a single spleen. The length of the left pancreas, which lay slightly anterior to the right, was equal to that of the combined right pancreas and spleen. A groove across the middle of the pancreas suggested that this mass also included both pancreas and spleen, but the serial sections showed that the whole was pancreatic in structure. The single spleen may be regarded as part of the vascular system which was here single.

The X-ray photograph indicates the presence of an opaque substance in the alimentary canal which was shown to consist largely of sand grains. Since this lay posterior to the pylorus it was not possible to determine through which mouth it had entered. A two-headed viper which lived in captivity for three days was found by Dorner to have died with the right mouth and stomach full of sand grains. This he attributed to an unsuccessful search for ants' eggs,

which are said to form the food of young vipers. Comparison of the condition of the fat body with that of a normal specimen of the same size and species might give some indication of the extent to which the animal had fed.

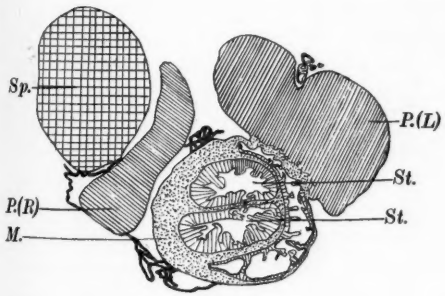


Fig. 3.

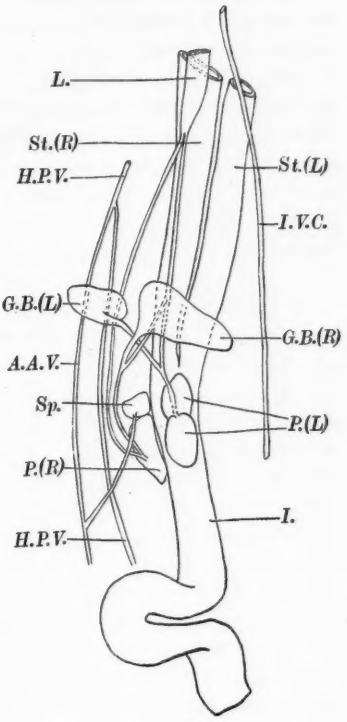


Fig. 4.

Text-fig. 3. Transverse section at the confluence of the two alimentary canals. *M.* circular muscle. *P.* pancreas. *Sp.* spleen. *St.* stomach. In figs. 3, 4, 5 and 6, (*R*) and (*L*) indicate that the organs belong to the right and left systems respectively.

Text-fig. 4. Ventral view of stomachs and digestive glands. *A.A.V.* anterior abdominal vein. *H.P.V.* hepatic portal vein. *G.B.* gall bladder. *I.* intestine. *I.V.C.* inferior vena cava. *L.* liver. Other lettering as in fig. 3.

The respiratory system

The two respiratory systems were independent and complete in themselves. The walls of the air sacs at the posterior ends of the lungs were very closely applied to each other, but no connection could be found between the two systems.

The vascular system

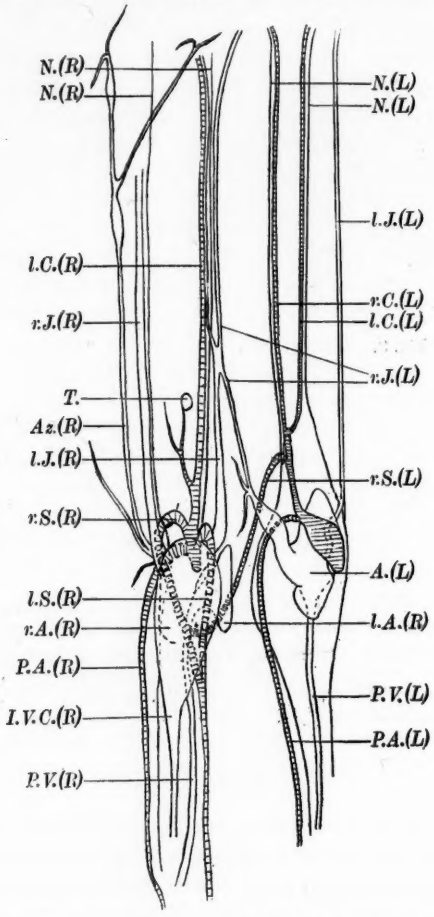
The disposition and the nature of the vessels was examined by dissection and was verified in serial sections of three regions:

(*a*) the hearts and arches;

(*b*) the junction of the left jugular of the right system with the right jugular of the left system;

(*c*) the transverse fold region.

There were two hearts lying in separate pericardia and two circulatory systems (text-fig. 5). In the following account the additional letter R or L before



Text-fig. 5. Ventral view of heart and main vessels. *A.* auricle. *Az.* azygos vein. *C.* carotid artery. *J.* jugular vein. *N.* vagus nerve. *P.A.* pulmonary artery. *P.V.* pulmonary vein. *S.* systemic artery. *T.* thyroid gland. *r.* right. *l.* left. Other lettering as in fig. 4.

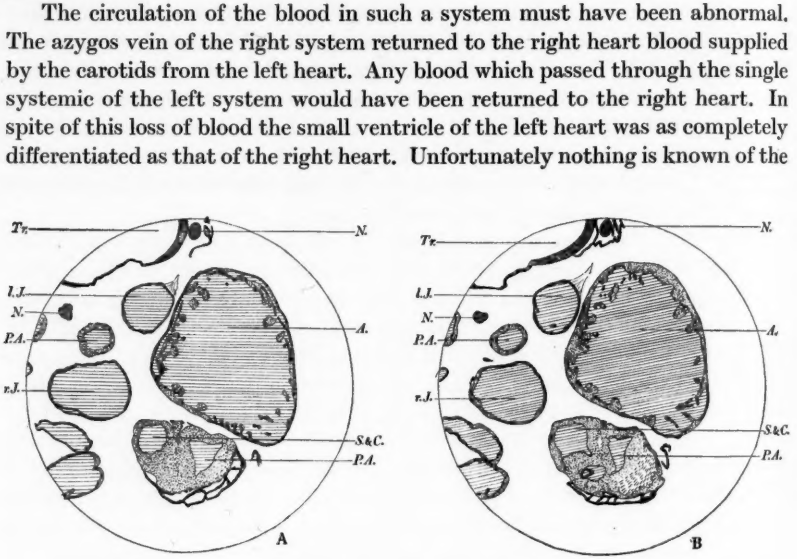
the name of a vessel indicates that it belonged to the system which served the right and left head respectively.

The right system was the more extensive, the heart was normal in size and position, and the most noticeable abnormality was a considerable enlargement of the right auricle which covered the ventricle. This auricle was fed by a normal inferior vena cava, right anterior vena cava and a rather smaller left anterior vena cava. A normal pulmonary vein emptied into the left auricle. The anterior azygos vein was enlarged and drained blood from each pharynx and the dorsal musculature near the transverse fold. The left jugular vein anastomosed with the right jugular of the left system and is discussed with that system. The ventricle, conus and arterial systems were normal. The pulmonary artery was thin walled and the left systemic artery had a diameter about five times as large as that of the right systemic artery. The right carotid was suppressed and supplied the thyroid gland in the usual manner.

The left system was incomplete, and the left heart, which was rather more than half as large as the right heart, was placed a little anteriorly. The ventricle was completely exposed and lay in a more than usually transverse direction. The only venous supply from regions posterior to this heart was through the pulmonary vein into a large anterior auricle. There was no trace of a posterior vena cava. The left jugular vein ran dorsally to the heart to open into a posterior swelling ventral to the pulmonary vein. The right jugular vein and the left jugular vein of the other system anastomosed slightly anterior to the thyroid gland. Anterior to the anastomosis the diameter of the jugular of the left system was about four times as long as that of the jugular of the right system, whereas posterior to the anastomosis these proportions were reversed. Thus the main supply appeared to be about sixteen times as great as in the other parts of the vessels and ran from the left head into the right heart. The anterior part of the left jugular of the right system was very closely applied to the carotid artery of the right system. The azygos was quite small and ran into the left jugular vein just anterior to a dilatation of this vessel. Dilatations of all three veins, pulmonary, left and right jugulars, opened into the large anterior auricle dorsal to the ventricle. This single auricle had two separate openings into the ventricle, which was normally divided. The serial sections show that from the ventricle there issued the normal three trunks (text-fig. 6 *b*); the pulmonary artery and the right systemic arch followed approximately normal courses, but the left systemic trunk was closed off before leaving the heart text-fig. 6 *a*), so that it was represented by a very small diverticulum of the ventricle. The right systemic trunk was elongated anteriorly, and slightly posterior to the level of the thyroid gland it gave off the right systemic artery equal in size to the corresponding vessel of the other system. The anterior branch from this trunk was slightly larger than the systemic artery and, dividing into two, formed equally and well-developed right and left carotids. The development of the right carotid may be connected with the fact that no trace of a thyroid gland could be found on this circulation. The right systemic artery

from the left heart passed dorsally to the left systemic of the other system to join the right systemic of the right system at almost 90°. Slightly posterior to this junction the right and left systemics of the right system united to form the dorsal aorta. Posterior to the heart there was thus one main arterial trunk and a single inferior vena cava returning all the blood to the right heart.

The circulation of the blood in such a system must have been abnormal. The azygos vein of the right system returned to the right heart blood supplied by the carotids from the left heart. Any blood which passed through the single systemic of the left system would have been returned to the right heart. In spite of this loss of blood the small ventricle of the left heart was as completely differentiated as that of the right heart. Unfortunately nothing is known of the



Text-fig. 6. Transverse sections through the left heart and blood vessels. A. 30 μ anterior to B. *Tr.* trachea. Other lettering as in fig. 5.

behaviour of this system from observations on the living animal. Since both ventricles were well developed it is probable that both functioned. There is nothing to indicate that they were synchronised, and since four vagus nerves were traced past the hearts they were probably subject to an independent nervous control. If the ventricles were in systole together but very little blood would have passed from one system into the other. On other and probably more frequent occasions blood would first be pumped by the right heart into the left carotids, and then blood from the left heart would be forced into the dorsal aorta. The volume of blood in the two systems would therefore be subject to fluctuations which would be of considerable significance in the very small left system. The existence of a venous connection between the two systems probably lessened the effect of this variation. This fusion did not appear to be part of the general fusion of the two heads and may have been brought about by a distinct developmental process.

The excretory and reproductive systems

The excretory and reproductive systems appeared to be normal.

DISCUSSION

Behaviour

Adequate records of the behaviour of such abnormal specimens would be of great value, but although several specimens have been kept in captivity (Wall, Dorner, Silly, Vsevolojsky, Borgert, Fischer) the records are too incomplete to make possible an attempt to correlate behaviour and anatomy except on one point. Most authors have considered only the independence or otherwise of the heads. When each has a complete set of receptor organs, a complete brain and normal musculature it is reasonable to suppose that the heads, being subjected to different stimuli, will behave independently. Strohl concluded that the evidence was conflicting, "les uns ont vu les deux têtes se mouvoir et happer toujours simultanément (Silly, 1841; E. C. Fischer, 1896); d'autres rapportent des observations contraires (Vsevolojsky, 1812; Dorner, 1873; Borgert, 1897; Reuter, 1921)." E. C. Fischer (1896) says clearly that "each head is endued with separate will power." The evidence from Silly is less definite. "Le lendemain matin—l'animal qui conservait encore un reste de vie me fut apporté, mais il mourut au bout de quelques instants." We can only conclude that the account of the similarity in behaviour of the two heads which followed was based on evidence supplied by the labourer who caught the animal. This is the only evidence that two separate heads behave simultaneously.

The movements of many posterior parts of Vertebrates are controlled by impulses originating in the head. This is especially clear in animals which progress by means of a wave of muscle contraction which passes along the whole body. Observations of such movements in the single region of double-headed specimens would be interesting. The only recorded observations are those of Borgert, whose viper executed rotatory movements continually either to the right or left.

The line of fusion and specific differences

Johnson (1901) reviewed the literature of double-headed snakes and paid special attention to the degree of bifurcation. His conclusions will be considered in the light of the rather more detailed account given in this paper.

1. "That the point of bifurcation of the vertebrae is more posterior than would be supposed from external examination."

It is clear that when the anatomy of the whole animal is considered there was a line, not a point, of bifurcation. This line was curved and passed from the dorsal surface at the level of the first neck band, through the vertebrae, the point of union of the right systemic arteries, the pylorus, and flattening out ran to the anus close to the ventral surface. Ventral to this line the animal was double, dorsal to it the animal was single. It is therefore possible to picture a

plane of separation bounded dorsally by the line of bifurcation. The inner layers of tubular organs, e.g. the alimentary canal, retain traces of bifurcation after the outer layers have assumed the normal condition.

On the basis of the rather inadequate published descriptions we may conclude that most of the specimens possessed planes of separation similar to that described above, but Strohl has figured an interesting double-headed snake belonging to the Museum of Natural History at Geneva in which the heads are partially fused, the vertebral columns are distinct, and the posterior third of the body bifurcated. So far as it is possible to form an opinion from the published photographs and description the plane of separation here passes through the dorsal side of the animal and is bounded ventrally by a curve similar in direction but placed more dorsally than that just described. That this simple condition is not universal is indicated by a specimen of *Tropidonotus sipedon* described by Wyman in 1865, in which the vertebral column was said to be double in the anterior, middle and posterior parts of the body and single in the second and fourth sections.

2. "That the point of bifurcation is most likely to occur in the cephalic half of the snake, between 6 and 13 per cent. of the entire length from the cephalic end."

If the first of Johnson's generalisations is modified as suggested above it will be impossible to find a simple ratio for the lengths of the double and single parts of the animal. To define the limits of the plane of separation requires more detailed study of the specimens than has been customary hitherto, but, since this plane of separation probably represents the original extent of bifurcation, comparisons would be valuable. Are the lines of bifurcation parallel to a given line? To what extent may the plane of separation be distorted?

3. "That this abnormality is more abundant in some species than in others."

Johnson considered but twenty-five cases. Strohl, who reviewed the whole subject again in 1925, extended this number to sixty-eight, and to his list we can now add:

Elaphe vulpina (Baird and Girard), 1 specimen; Amaral, 1927.
Lampropeltis getulus getulus (L.), 2 specimens; Amaral, 1927.
Natrix sipedon fasciata (L.), 2 specimens; Amaral, 1927.
Bothrops atrox (L.), 3 specimens; Amaral, 1927.
Crotalus terrificus (L.), 1 specimen; Amaral, 1927.
Pituophis sayi (Syn. *Coluber melanoleucas*, Daud.), 1 specimen; Pope, 1927.
Thamnophis sirtalis infernalis 1 specimen; Fisher, 1928.
Coluber (*Zamenis*) *florulentis* 1 specimen; present paper.

Most of these are new species to show the abnormality. Although thirty-three of the eighty belong to the genus *Tropidonotus* and nineteen of these to the species *T. natrix*, it would be rash to assume that some genera or species are more susceptible to duplicitas anterias than others. The phenomenon is widely distributed taxonomically and geographically. The groups from which most

specimens are known are the most widely distributed in regions from which records are likely to be kept. The habits both of snakes and men will introduce factors to invalidate any conclusions drawn from a simple consideration of the numbers of different species recorded. Confirmation of this generalisation must await the results of experimental rearing of different species.

Causes of the abnormality

Most of the descriptions of specimens have been followed by a description of an hypothetical early stage or by other hypotheses designed to explain the origin of the abnormalities. Such hypotheses were considered by Strohl, who concluded that it may be possible to classify cases of double-headed snakes on the causes of their origin. Apart from the improbability that they arise from more than one cause, it is better to work on the simpler hypothesis that double monsters arise from a single cause until the evidence makes it necessary to adopt the more complex hypothesis. It is, moreover, highly probable that the three monsters from a brood of 120 *Zamenis constrictor* (L.) described by Mitchill, and which exhibited very different degrees of bifurcation, all owed their abnormality to the same cause. A review of the hypotheses which have been suggested makes clear the fact that in general successive writers have referred the abnormality to earlier and earlier stages of development, e.g.

(1) Dorner (1873) assumed the fusion of two embryos.

(2) Tornier (1901) suggested regeneration after an embryonic lesion.

(3) Spemann (1919) refers to division of the dorsal lip of the blastopore.

(4) Dareste (1891) Wilder (1908) and Rabaud (1914) to irregular gastrulation.

(5) Gräper (1931) relates all chick double monsters to pregastrula streamings of protoplasm.

Of these Tornier alone refers to a possible external influence different from that acting in normal circumstances but which might occur under natural conditions.

Examination of abnormal but more or less mature animals is unlikely to provide sufficient evidence to show whether such abnormalities are to be assigned to several causes or to one. Comparison of the anatomy of naturally occurring specimens with the anatomy which must be assumed to follow from the various hypotheses may serve to check the false though it cannot verify the correct hypotheses. It is difficult to explain the structure of the specimen herein described on Tornier's hypothesis of wound regeneration. The main axis which should represent the original animal which regenerated is different according to whether the vertebral column or the blood system is considered. The left vertebral column appears to be continuous and to bear a branch on its right side. On the other hand the right heart is connected with a much more complete blood system than is the left. Even if we suppose that the difference in the vertebral columns resulted from a more extensive use of the left head this must have been at least equally well developed when use commenced. In

Tornier's diagram of a hypothetical two-headed snake more detail is shown in the original than in the regenerated skull. This is not mentioned in the text and it is therefore not clear if a deficiency of the regenerated head was indicated. The X-ray photograph and the Spalteholz preparation of the subject of this paper both indicated a normal structure for the two heads.

More recently Gräper (1931) has identified the early stages of duplicitas of all kinds in the chick egg with abnormal protoplasmic streamings preceding the formation of the primitive streak. Such streamings are not all hypothetical, for Gräper has recorded some of them with his stereo-cinematograph. He explains duplicitas anterias by the setting in of two streamings eccentrically situated on the germinal disc. Streamings which would normally each be sufficient to form one embryo meet, each turns aside in two halves to form a new anlage with a similar half streaming from the other side (text-fig. 7). Since the positions are eccentric the material from one side will be exhausted before that from the other, leaving the more posterior region single. Although each of the resulting heads is composed of material of different streamings Gräper has carried the analysis back so far that we could not expect to detect this in the adult. In one point, however, our specimen does not appear to receive a full explanation on Gräper's hypothesis. The two hearts are both formed from material of different streamings, but each one is composed of right and left anlagen in the normal relations. When the material of the shorter side gives out it would be expected that the right systemic arch of one system would join the left systemic arch of the other. In the specimen, however, in spite of the fact that the right systemic from the left heart must pass close to the left systemic from the right heart it goes further and joins the right systemic from this heart (text-fig. 8).

Bataillon and several subsequent workers have pointed to the effect of such external conditions as delay in fertilisation and the presence of foreign substances in the environment. Strohl has also pointed out that most of the specimens of double-headed snakes have been caught when a few days old at the end of the breeding season. Of the specimens described since his review information is available for two specimens only. Pope's *Pituophis sayi* (Schlegel) was collected in the summer of 1902 at Sylvan Grove, Kansas. Fisher's *Thamnophis* was 2 or 3 days old when found dead in California on 4 September, 1926. The specimen described in this paper was caught near Cairo, Egypt, probably during 1925, but no information could be obtained as to its date of capture.

The factors which may be involved in this hypothesis are:

(1) Ovarian exhaustion.

(2) Prolonged sojourn in the oviduct and

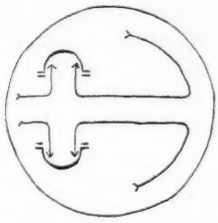
(*a*) toxic effect of secretions, products of metabolism or of destruction of other eggs;

(*b*) delayed fertilisation and consequent over-ripeness of ova.

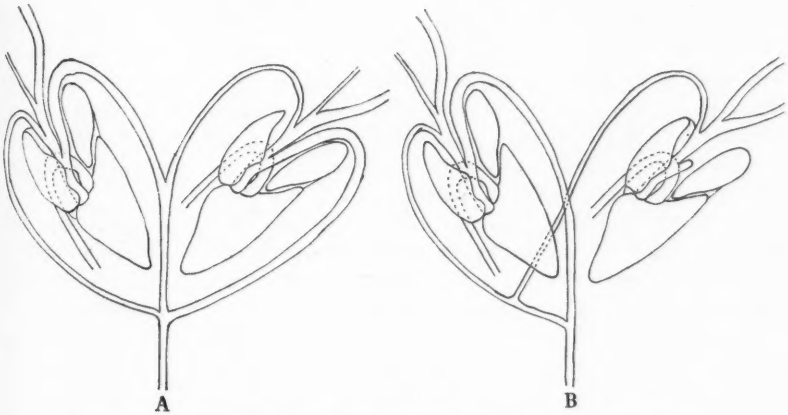
(3) Unusual environmental conditions during development.

(4) Late hatching may be the effect and not the cause of the abnormality.

The first of these factors is not known to have any effect. Both factors included under (2) are known to result occasionally in abnormal development. The cause may be the same in both cases. Abnormal embryos always represent a small proportion of the broods, and some of the specimens belong to viviparous species. It is therefore probable that neither the climate of the nest nor the district is responsible for the abnormalities. The second is therefore the most likely factor to be involved.



Text-fig. 7. Pregastrula streaming which results in duplicitas anterior (Gräper). = Heart rudiment. ∩ Anterior border of embryo.



Text-fig. 8. Ventral view of hearts and main arteries. A. As required on Gräper's hypothesis. B. As in the specimen.

CONCLUSIONS

1. The study of the anatomy of a double-headed snake indicates that the boundary of a plane which separates the two heads is well defined but may be distorted. Consideration of this plane may provide some evidence of the manner of origin of the two parts. The example described in this paper does not

agree with the regeneration hypothesis put forward by Tornier, nor does it support Gräper's hypothesis of streaming.

2. Two related developmental phenomena may be distinguished:

(*a*) development of the embryo modified by an unusual stimulus,

(*b*) the readjustment of systems to make a viable entity of this unusually organised matter.

The first of these events would result in a specimen single on one side, completely double on the other side of the line of bifurcation. The second process becomes much more important at the end of the embryonic period, especially in the complex systems which pervade the whole animal. Doubling of the alimentary system does not introduce important difficulties, and hence little modification of the simple condition is necessary although in the specimen described a diverticulum of the intestine carried the secretions from the left pancreas into the intestine. In the vascular system the jugular anastomosis which occurred well to the ventral side of the line of bifurcation stood out as an exception to the main scheme of fusion, and since it can be shown to be of considerable functional importance it was probably a secondary development which converted an ineffective into an effective system.

The commissure connecting the roots of the last pair of spinal nerves to issue ventral to the line of bifurcation is also considered to have been such a secondary development. Thus the vascular and nervous systems may have followed the normal development in the separate parts until the two sets of systems interfered with each other. They then appear to have been made workable by the development of suitable anastomoses, a process for which no allowance is made in the current hypotheses of experimental embryology. Further investigation of this adjustment may throw some light on the origin of variation, i.e. of individual differences which cannot be attributed to germinal differences and which may be adaptive.

3. The study of the origin and development of two-headed snakes deserves experimental treatment especially by the incubation of overripe or of chemically treated eggs. Fortunately *Tropidonotus natrix*, at once plentiful and innocuous, appears to be susceptible to the causes of this malformation.

In conclusion I wish to express my thanks to Prof. J. Stanley Gardiner, to whom I am indebted for the specimen and for permission to dissect it thoroughly, to Mr C. Forster Cooper and Mr C. F. A. Pantin for help and advice, to Mr W. Parker, of the British Museum, for the identification of the species, and to Dr Barclay for the X-ray photograph.

EXPLANATION OF PLATE

Figs. 1 and 1*a*. Dorsal and ventral views of the *Coluber florulentis*.
Fig. 2. X-ray photograph of *Coluber florulentis*.

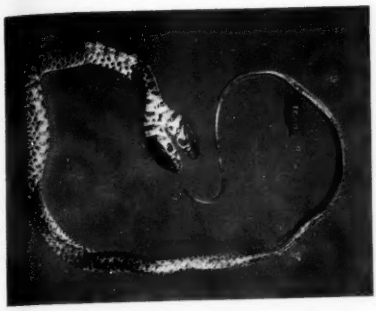


Fig. 1.

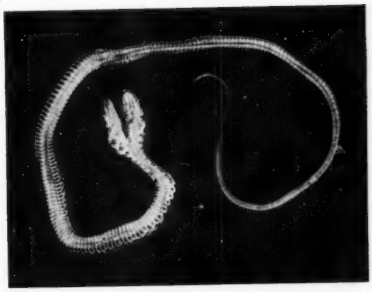


Fig. 1*a*.

Fig. 2.

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ANATOMICAL NOTES

THE PREPARATION OF SERIAL MACROSCOPIC BRAIN SECTIONS FOR TEACHING PURPOSES

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At the summer meeting of the Anatomical Society I had the pleasure of demonstrating a series of sections of the human brain which I had prepared and mounted for museum purposes. My object in showing these specimens (which I was encouraged to do by Prof. Le Gros Clark) was to bring to the notice of the members of the society the vivid pictures obtained by Mulligan's(1) method of brain staining and the great use of this method for museum or teaching purposes. Sincke's(2) method of staining, which was elaborated by Mainland(3) in 1928, has been used for some years in this country. It has been recognised, however, that fading occurs and that the stain loses its intensity in a comparatively short time. Mulligan's method does not appear to be open to this objection, and at the same time it gives a contrasted black and white result which is very striking.

The demonstration created sufficient interest to make me feel that it was worth recording the details of the technique in the hope that others might be induced to prepare sections in a similar manner. Of the value of such sections to the student there can be no doubt. There is the further advantage that a complete series of sections can be both rapidly and easily prepared.

Cutting, staining and mounting of sections

A brain which has been thoroughly fixed in formalin is well washed in running water for 12–24 hours.

Before sectioning the brain must be enveloped by some suitable material which will retain all the parts in their correct inter-relationships. Gelatin appears to be the most suitable agent for this purpose, though it has the disadvantage of subsequently taking up the stain rather deeply. Sheets of gelatin are placed in cold water overnight: in the morning the surplus water is poured off and the gelatin is heated in a double saucepan until it is melted. It is essential to have a sufficient quantity of gelatin to make a bath which will ensure that the brain is completely covered. It is preferable to leave the pia and the arachnoid membranes intact over the surface of the brain; not only do they help to hold the parts together, but, after sectioning, a complete picture of the main blood vessels and of the undisturbed chorioid plexuses is obtained.

The washed brain is placed in the bath of melted gelatin which is forthwith allowed to cool gradually. When cold it is cut out from the saucepan as a solid block and the gelatin is trimmed a little if necessary.

In default of an expensive brain macrotome, a very simple method of cutting serial sections was employed. It was first suggested and used by Prof. J. T. Wilson a few years ago. An ordinary bread slicing machine with a circular knife rotated by hand is used. Though apparently rather crude, the results in practice are excellent provided that a thick coat of gelatin surrounds the brain. A brain which has not been embedded can be cut by this method, but the slices are not of even thickness nor can they be handled so easily afterwards, since it is practically impossible to avoid the separation of isolated pieces within the section.

In cutting the sections there are one or two points to be observed:

(*a*) The operator requires an assistant to turn the handle and to collect the sections, whilst the operator himself should hold the brain and keep a steady pressure on it as it is cut. Firm pressure is particularly necessary to counteract the marked downward drag of the knife on the tissue.

(*b*) The knife is moistened with glycerine occasionally to minimise the drag as far as possible.

(*c*) A glass plate or a stiff piece of cardboard should be held parallel to the knife and a short distance away from it while cutting so as to provide a support and prevent the section from twisting over and tearing.

(*d*) If horizontal or sagittal sections are required, it is advisable to rivet a larger plate on to that supplied with the machine in order to provide an ample area for steadying the whole cut surface of the brain.

In this way a complete series of sections can be cut rapidly. The knife can be adjusted to cut at any desired thickness. The optimum thickness of section appears to be about 3 mm.: this allows one to handle the section afterwards without much fear of breaking it.

As the sections are cut they are placed in sequence on flat trays. When the series is complete, each section is blotted and numbered by painting on some convenient place in the white matter with Indian ink, or, better, with the acetone-ether-Indian ink mixture used by Da Fano (4) for numbering celloidin sections as this dries more rapidly.

The slices are next covered with 10 per cent. formalin for some hours. As emphasised by Mulligan, this refixation of the cut surface is important.

After washing in running water overnight, the sections are stained by Mulligan's (1) method. Complete details are given in his paper. I did not find it necessary to put the sections in distilled water before commencing to stain, nor did I find it necessary to make up the solutions with distilled water as Mulligan recommends. I used tap water throughout, and was unable to convince myself that there was any real difference in the results.

The sections when stained may be freely handled; a little care is necessary, as any sort of scratching against a rough surface will remove the stain which is only a superficial one.

The gelatin stains black. It can either be trimmed or it can be removed completely by careful dissection with a cataract knife. In some places it will be found that considerable amounts can be cleanly removed by breaking it off with the fingers.

The sections are mounted in sequence on matt opal glass plates by means of a thin film of 20 per cent gelatin. The surface of the sections is covered with very thin gelatin. After allowing the gelatin to harden superficially in the air, the plates are placed in shallow trays and covered with 10 per cent. formalin to complete the hardening. Large quantities of bubbles appear on the surface of the sections, but they can be neglected as they disappear after a few hours.

The opal glass plates used measure 11 × 16½ in.; they comfortably accommodate four transverse or two horizontal sections each. Two plates are mounted, back to back, in each glass jar. The space between the plates is packed with absorbent cotton-wool. I have been using rectangular glass jars measuring 5 × 13 × 17½ in.

As only the surface of the sections is stained, it must be protected from abrasion against the sides of the jars: this is effected by means of "buffers" of plasticine placed at the corners of the plates.

The jars are filled with 70 per cent. alcohol and sealed up in the usual way. Though Mulligan recommends 70 per cent. alcohol for preserving the sections, I have kept several in formalin for some months without any obvious ill effect. I am inclined to believe that the sections could be kept indefinitely in 5 per cent. formalin.

Results of this method

The method is rapid and the stain should be permanent. Prof. Le Gros Clark has had sections similarly stained in a strong light for over a year without any visible change.

Mulligan's method is not so delicate in its results as some of the other methods of macroscopic brain staining, e.g. Sincke's (2): this is particularly evident in the thalamic and the hypothalamic regions. The red nucleus, for example, is outlined but remains unstained; of the reason why the red nucleus in particular should fail to take up the stain I am ignorant. Far from detracting from its value, however, this comparative lack of delicacy appears to me to enhance the use of the method for teaching and demonstration purposes. The main masses of grey matter stand out extremely distinctly as black areas on a light background.

Incidentally, I think that a modification of Mulligan's method might advantageously be used by students in the dissecting room as a routine during the later stages of a brain dissection. It reveals the outlines of the basal ganglia, the inferior olivary nucleus, the dentate nucleus, etc., very clearly, so that a student who is dissecting the brain for the first time will get a much more convincing demonstration of such structures than he does in the unstained brain. Should a slice be inadvertently overstained, the unstained surface is easily re-exposed by gentle scraping.

I would suggest the following modification as being suitable for routine use on account of its rapidity and its simplicity. The phenol, tannic acid and iron alum solutions are made up in the strengths given in Mulligan's paper (1), tap water being used instead of distilled water. The method is economical, as the solutions can be used repeatedly. The brain slice is then treated as follows:

(1) Wash in running water, 1 min.

(2) Carbolic solution, 1 min. This solution is used cold since the practical difficulties of keeping it at a constant temperature of 60° C. for indefinite periods would obviously defeat the object of this simplified method.

(3) Wash, 1 min.

(4) Tannic acid solution, 1 min.

(5) Wash, 1 min.

(6) Iron alum solution until sufficiently dark, usually about ½ min. is ample. Wash in running water. Once the grey masses are clearly visible the section should be removed from the iron alum solution and washed immediately, otherwise a diffuse staining of the white matter will result.

Naturally the differentiation obtained by this method is not so good as with the original method, but I have tried many slices this way and I am sure that it is of distinct value for the use of students.

Fissural and convolutional anatomy of sections

When annotating serial sections cut and stained in the way described, one gets into insuperable difficulties in attempting to name the sulci in each section. Some, of course, are obvious, but it is impossible to be sure of many others.

To overcome this difficulty the following method was devised and has proved successful.

The formalin-fixed brain is cleaned of all its membranes, care being taken to remove them completely from the depths of the sulci. It is then photographed (*a*) from each side, (*b*) from below, (*c*) from above and (*d*) from behind.

The sulci are now painted in different colours. The brain should first be dried with dusters as much as possible so that the colours shall not run into each other. The paints I have used for this and many other purposes are Reeves' "Tempora" colours which were recently recommended by Congdon (5). The advantage of these paints lies in their brilliance and in the great range of colours obtainable. The colours

are chosen so that only markedly contrasted ones are used for sulci which lie close to one another. The brush is loaded with colour (which is diluted slightly with egg albumen or with Reeves' "Tempora" medium) and pushed well down to the bottom of the sulcus. The object is to load the sulcus with as much colour as possible: the colour should also be carried a short distance on to the surface of the brain over each lip of the sulcus.

As each sulcus is coloured, so the colour is painted on the corresponding sulcus in the photographs. A complete key is thus obtained for reference after the brain has been sectioned.

When the painting is finished the whole brain is put into 90 per cent. alcohol in order to precipitate the albumen and fix the paints. After a few hours in the spirit the brain can be handled gently without fear of disturbing the colours.

The brain is then put in a gelatin bath and cut into sections as described above. The colours show up well on the cut surface and the sulci are readily identified from the key photographs.

Annotation of the sections

A photograph is taken of each section of the series and enlarged to actual size. An Indian ink outline is made and the bromide print is bleached out. The drawing may be coloured as desired. After mounting on cards and annotating, the series can be bound as an album which is kept near the sections for reference. The drawings are preserved from damage by being covered with sheets of "Cellophane."

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A MODIFICATION OF RANSON'S SILVER NITRATE METHOD FOR DEMONSTRATING AXIS CYLINDERS

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Of all the impregnation methods available for the histological study of the peripheral nervous system, the technique of Ranson(1) is perhaps one of the most valuable to the average worker in that it combines comparative simplicity with a tolerable certainty of a good result, and is in addition applicable to the making of serial paraffin sections. The method was originally designed to show the non-myelinated fibres in mixed nerves, but under suitable conditions nerve endings of all kinds can also be well demonstrated, as well as nerve cells and myelinated fibres.

The great disadvantage of the technique, however, is the necessity for fixation in absolute alcohol and ammonia: this treatment renders certain tissues extremely brittle and difficult to cut in serial section, and it also limits the application of the method to tissues obtained in fresh condition. An investigation was accordingly made of the various stages in the process in an endeavour to find a modification that would overcome these difficulties and yet give the uniformly satisfactory results of the original method, thus increasing its range of usefulness.

Ranson's original method

This is as follows:

Fix small pieces of tissue for 48 hours in absolute alcohol, 99 parts; concentrated ammonia, 1 part.

Rinse in distilled water.

Transfer to pyridine for 24 hours.

Wash in many changes of distilled water for 24 hours.

Transfer to 2 per cent. $AgNO_3$, in the dark, at 35° C., for 3 days.

Rinse in distilled water.

Reduce for 1 day in 4 per cent. pyrogallol in 5 per cent. formalin.

Wash in water.

Dehydrate, clear, and embed in paraffin wax.

(*a*) *Fixation.*

Of the common fixatives other than alcohol none gave satisfactory results except formalin. Fixation in the usual way with 7 per cent. formalin in tap water is not in any way detrimental to the subsequent processes, provided that the tissue is after fixation very thoroughly washed in running tap water for at least 12 hours. This point is important because uniform impregnation with silver salts is much helped by a slight degree of alkalinity. Excellent results were obtained by this means even with human brain tissue that had been lying in formalin for 6 months, the washing in this case being extended to 24 hours. After washing, the tissue may be put straight into pyridine, as an intervening treatment with absolute alcohol and ammonia does not seem to have any beneficial effect. The addition of ammonia to the fixing formalin solution is of no apparent value.

(*b*) *Action of pyridine.*

The treatment with pyridine is essential because it prevents the impregnation of nuclei, of connective tissue fibres, and of capillaries, and should be carried out for 1–3 days according to the size and density of the tissue. Fixation by pyridine alone was not found to be very adequate: it causes much shrinkage and in addition renders the tissues extremely brittle.

Before treating with $AgNO_3$ it is essential that *all* pyridine should be removed by distilled water, and this can only be effected by giving repeated washings with fresh distilled water for about 24 hours.

(*c*) *Impregnation with* $AgNO_3$.

The duration of the treatment with 2 per cent. $AgNO_3$ is not very important, but it should be not less than 3 days and as a rule not more than 5 days, and must be carried out in the dark at 37° C. If tissues are left in $AgNO_3$ for as long as 7 or 8 days there is a tendency for a precipitate to appear in them.

(*d*) *Reduction.*

After washing, reduction in the pyrogallol-formalin mixture should be carried out for at least 6 hours, and preferably for 10 hours or even longer for large blocks: if the solution becomes dark or cloudy it is important that the tissues should be transferred to fresh fluid. Reduction should not be accelerated by warming, as this causes blackening and hardening of the outside of the block and consequent lack of reduction inside.

There does not seem to be any particular reason for using 5 per cent. formalin, as reduction with 4 per cent. pyrogallol in distilled water is quite effective, and treatment with the formalin alone (even in a strength of 10 per cent.) gives very incomplete reduction.

(*e*) *After treatment.*

Dehydration should be carried out rapidly as the tissues are apt to become brittle in alcohol. Paraffin sections should be not more than 10μ thick. If the yellow colour of the background is objected to, sections can be toned in the usual way with 0·2 per cent. $AuCl_3$, but the resulting picture does not show the nerve fibres and endings in quite such sharp contrast as before. The material can be embedded in celloidin in the usual way if this is preferred to paraffin.

Application of the method

(1) *Nerve fibres in muscle.*

Blocks of tissue should not be more than 3–4 mm. thick. Fixation in formalin renders the muscle less brittle than does absolute alcohol and is therefore more suitable for serial work, and the impregnation is equally good in both cases. Motor nerve endings, and sensory spindles and tendon organs, are sharply picked out in sections, and show best if the muscle fibres are cut longitudinally, this plane of section being also the most useful for following the distribution of nerve fibres. Incidentally the detailed structure of the muscle fibres is also shown exceedingly well.

(2) *Cerebellum and cerebrum.*

Fixation with absolute alcohol shortens the process, but does not seem to have any other real advantage over formalin. Sections obtained by this method compare quite favourably with successful Bielschowsky preparations, and the technique is much shorter and simpler, and serial sections are easily accomplished. The whole brain of a human 36-week foetus was treated by this method, after fixation in formalin: the smaller blocks were embedded in paraffin wax, and the larger in celloidin: the detail was found to be very good in both series.

(3) *Whole brain.*

As shown by Hüber and Guild (2) Ranson's method is applicable to whole brains of small animals. A good method is to expose the dorsal surface of the brain and fix *in situ*, dissecting out later. Excellent results were obtained with rabbit foetuses of about 16 days and with new-born kittens, the brains being cut in serial sections of 10–12 μ thickness.

(4) *Whole embryos.*

Whole embryos up to about 30 mm. can be impregnated quite successfully, but if decalcification is necessary de Castro's method (3) (chloral hydrate modification) is preferable, although Hüber and Guild obtained good results with 7 per cent. HNO_3 after alcohol fixation. A human embryo of about 60 mm. was cut into four blocks after fixation in absolute alcohol had been carried out for 2 hours, and the blocks were then treated by the standard Ranson technique, impregnation and reduction being excellent throughout. When a variety of tissues, such as those of a foetus, is being dealt with the pyridine treatment should last not less than 2 days. Developing bone present in such embryos is also impregnated and appears black.

Summary

A modification is given of Ranson's $AgNO_3$ method for the staining of axis cylinders which increases its range of usefulness.

REFERENCES

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(2) Hüber, G. C. and Guild, S. R. (1913). *Anat. Record*, vol. vii, p. 253.
(3) de Castro, F. (1926). *Travaux du Laboratoire de Recherches biologiques de l'Université de Madrid*, t. xxiii, fasc. 4, p. 427.

REVIEWS

A Companion to Manuals of Practical Anatomy. By E. B. JAMIESON, M.D. Third Edition. Pp. 654 + xxxv. (Humphrey Milford, Oxford University Press, London.) 1932. 12*s.* 6*d.* net.

Although the second edition of this useful little book appeared in 1925, and was reprinted in 1928 and 1931, the present third edition has been very thoroughly revised and, in a large part, rewritten. The size of the book has been increased by about one hundred pages, but the book is still of a very useful, serviceable form. The new matter, including that dealing with the central nervous system, is excellently set forth and very readable.

Although the B.N.A. terminology has been retained, the author is to be congratulated upon retaining such terms as "axis" and putting the B.N.A. term in brackets.

Some thirty pages are devoted to embryology and this is a very excellent condensed account of all the important factors which are concerned in human development.

The book should prove even more popular than its predecessors, and its value is not limited to the student of anatomy, but should be a book of ready reference to physicians and surgeons as well.

A Synopsis of Surgical Anatomy. By ALEXANDER LEE MCGREGOR, F.R.C.S. (Bristol: John Wright & Sons, Ltd.) 1932. Pp. xiv + 609. 17*s.* 6*d.* net.

This is indeed a most useful book and one which is crammed with information. It will take its place with the other two well-known books of the Synopsis series which have been written by Hey Groves and Tidy.

From beginning to end, the book is written in a clear, stimulating fashion, illustrated with many excellent black and white drawings, quite a number of which are quite original.

The book is divided into two parts; the first is devoted to the anatomy of the normal, while the second deals with the anatomy of the abnormal. This is a novel, yet excellent way of bringing out the essential features of surgical anatomy, and in no other book on the subject can be found such a mine of information.

We have no hesitation in agreeing with Sir Harold Stiles, who has written the foreword to the book, that it will be welcomed alike by the student, the surgeon, and the teacher of surgery.

THE DEVELOPMENT *IN VITRO* OF YOUNG RABBIT EMBRYOS

By C. H. WADDINGTON[1] and A. J. WATERMAN[2]

From the Strangeways Research Laboratory and Laboratory of Experimental Zoology, Cambridge

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INTRODUCTION

Very little experimental work has as yet been performed on the early stages of the mammalian embryo. The two main methods of experimental analysis, isolation of primordia and transplantation of fragments into different situations in the embryo, which have been applied with such success in the Amphibia, both present great technical difficulties when applied to the embryos of warm-blooded animals.

In the case of the bird the chorio-allantoic membrane of the developing embryo has been successfully used as a place for isolation of primordia (Hoadley, 1924, and others) and of portions of young blastoderms (Hoadley, 1926; Willier & Rawles, 1931). Recently Waddington (1930, 1932, 1933*a*, 1933*b*) has shown that young chick embryos may be successfully grown for several days on the surface of coagulated plasma and embryo extract. With this technique it is possible to perform various types of transplantation and deficiency experiments which are not possible with the former method. An outline of the process of determination of the embryonic axis in the bird, comparable to that worked out by Spemann and his school for the Amphibia, has been obtained in this way.

It is possible to isolate primordia of the rabbit embryo on the omental bursa of young or adult rabbits, in which environment the explant is incorporated by the tissues of the omental wall, and invaded by proliferations of host capillaries (Waterman, 1932*a*): the primordia exhibit a degree of independent self-differentiation comparable to that of control embryos of the same temporal age (Waterman, 1932*b*). Explants to this organ have given better results than others to various other regions of the adult.

[1] This work was done while I was in receipt of a part-time grant from the Medical Research Council, for which I should like to express my thanks.

[2] Fellow of the Commission for Relief in Belgium Educational Foundation 1931-2.

I wish to thank Dr H. B. Fell for the courtesies extended to me at the Strangeways Research Laboratory.

Rabbit eggs have been grown in tissue cultures with marked success (Pincus, 1930), while Maximow (1925) has described the differentiation taking place in isolated pieces of young rabbit embryos grown *in vitro*. The *in vitro* technique has also been used by Brachet (1912, 1913) for the study of the development of entire rabbit blastocysts.

In an attempt to find a cultivation method which would make possible transplantation experiments on mammalian embryos, Waddington (unpublished data) found that young rabbit embryos of 8–9 days of development will live on the surface of plasma clots composed of adult chicken plasma and a saline extract of chick embryo and will undergo some further growth and differentiation. This was sufficiently encouraging for the authors to pursue the subject further. Various stages of the rabbit embryo, from the late pre-primitive streak stage to that of 2–4 somites, have been explanted to the surface of plasma clots. The results secured from these experiments constitute the material described in this paper.

Portions of these early stages have also been transplanted between the epiblast and endoderm of chick and duck embryos in the definite primitive streak and head process stages. Brachet's experiments on the culture of whole rabbit blastocysts have also been repeated by one of us (Waterman) with various modifications of technique. These experiments will be described in detail in subsequent papers. It is sufficient at the present time to state that the blastocysts also will live and undergo some differentiation in this foreign medium. Development is markedly slower than the control and usually abnormal after a certain stage has been reached, depending upon the age of the blastocyst at the time of explantation.

MATERIALS AND METHODS

The technique used in the present experiments is the well-known watch-glass method of tissue culture *in vitro*. Equal amounts of adult chicken plasma and of a saline extract of a chick embryo of 8–9 days' incubation are thoroughly mixed in the bottom of a watch-glass and the plasma allowed to coagulate. The watch-glass is itself enclosed in a covered Petri dish and rests upon a ring of cotton wool moistened with sterilised distilled water to prevent evaporation of the culture.

The embryos are removed from the uterus into a separate dish and then transferred together with some saline solution to the surface of the clot. After the embryo has been oriented with the dorsal side uppermost and carefully spread out flat with fine needles, the saline solution is gently removed. It is possible to explant embryos almost entirely freed from the surrounding trophoblast, but this is not usually advisable since the adjacent trophoblast, if carefully spread out, prevents the embryo itself from curling during the first few hours of culture. Even so the culture undergoes considerable shrinkage and thickening, which often results in marked distortion of the developing embryo.

All operations have been performed at room temperature without any

effort to maintain a constant body temperature. Embryos have sometimes been kept in the refrigerator for periods ranging from 4 to 12 hours before being transferred to the clot. If the embryo is injured by this radical lowering of temperature it is not apparent either in the appearance of the culture as a whole or in the degree of differentiation exhibited by the embryo. Except for some retardation of the onset of development, the embryos thus treated compare favourably with those which were transferred immediately to the clot. It remains to be seen whether the maintenance of a high temperature and transference to a warm clot will give still better differentiation.

A saline extract of rat embryo of approximately 14–15 days' growth *in utero* has been substituted for the chick-embryo extract in the culture medium. In these experiments no effect was noticeable as regards the differentiation undergone by the embryos. Chicken embryos have also been cultivated satisfactorily on media made up with rat embryo extract.

It will be remembered that Brachet obtained similar results with both adult male and adult female rabbit plasma. Similarly, for the omental grafts of primordia (Waterman, 1932*b*), male or female, young or old, rabbits were used as hosts with no apparent effect on the differentiation obtained. In view of these facts, it seemed probable that the embryos would show considerable tolerance for foreign plasma, and since, as is well known, the use of mammalian plasma presents certain technical difficulties, we have in these experiments used chicken plasma, which has proved so satisfactory for the cultivation of most types of tissues by the hanging-drop method. Control experiments with rabbit plasma have not yet been made, but the results obtained in the cultivation of blastocysts by Brachet's method, using chicken plasma, compare favourably with Brachet's own results, using rabbit plasma, and it is probable that in the watch-glass cultures, the substitution of a soft rabbit-plasma clot for the hard chicken-plasma clot would have deleterious mechanical effects which would more than counterbalance any beneficial action of the homologous plasma.

The cultures have been grown for varying lengths of time, ranging from 1 to 5 days, without change of the medium. Chick embryos develop rapidly in culture, and the liquefaction of the clot is such that it is not feasible to grow them more than 2 days. In the case of the rabbit embryos, however, very little liquefaction of the clot occurs even after 5 days of culture. Moreover, development is much slower and the culture never attains any considerable size. Efforts have been made to change the medium after 48 hours, but the resulting injury has always resulted in immediate death and degeneration. The embryos are extremely delicate, and it seems almost impossible to separate them from the old clot without injury to the lower layers of tissue. Improvements in technique will, it is hoped, minimise this difficulty.

The stages used in these experiments range from the late pre-primitive streak to the stage of 2–4 somites, approximately 6–8 days' growth *in utero*. Up to approximately 7 days of growth the entire blastocyst may be removed

with or without puncturing. The embryonic disc may be isolated with little difficulty from the surrounding trophoblast. Generally, however, some of this tissue remains adherent; in fact it is better for the experiment if the immediately adjacent trophoblast is not removed. It facilitates flattening the embryo and usually prevents the curling or folding which is so detrimental to differentiation.

After approximately 7 days, the blastocyst can no longer be removed entire, as implantation is initiated at this time and the blastocyst is so large that any pressure ruptures it. The embryo is therefore isolated by tearing apart the uterine wall with fine forceps along the median line of the unattached surface. The flaps are then held apart while the embryo is isolated with fine scissors.

Needless to say the strictest precautions against infection must be taken in every phase of the experiment.

The technique of transplanting portions of the primitive streak and two-somite stages between the epiblast and endoderm of the chick embryo is similar to that already described by Waddington (1932).

Cultures have been fixed in Bouin's solution, and the whole mounts stained in Delafield's haematoxylin.

DESCRIPTION OF EXPERIMENTS

A classification of early embryos according to their age is of little use; for instance, after exactly 7 days' development *in utero*, counting for the time of copulating, the embryos from one female were in the primitive streak stages, from another in the pre-primitive streak stage and from a third in a pre-somite stage. For this reason the experimenter can never be certain of the exact stage he will find in spite of the fact that the time from the minute of copulation is known. Various factors may be postulated to account for this: possibly the length of the interval between copulation and fertilisation is important. Further, even within one uterus, not all of the embryos are of the same stage of development and this discrepancy becomes more noticeable in younger stages such as the ones used in the present experiments. After 10 or 12 days of development *in utero* the differences in development tend to disappear so that all of the embryos look quite alike.

The stages used in the experiments have therefore been classified according to stage of development and not according to age, as follows (fig. 1):

(*a*) Pre-primitive streak	fig. 1, XG
(*b*) Primitive streak:	
(1) Stage of posterior thickening	fig. 1, XE
(2) Short	
(3) Medium	fig. 1, XL
(4) Long	
(*c*) Pre-somite	fig. 1, XK
(*d*) Somite	fig. 1, XB

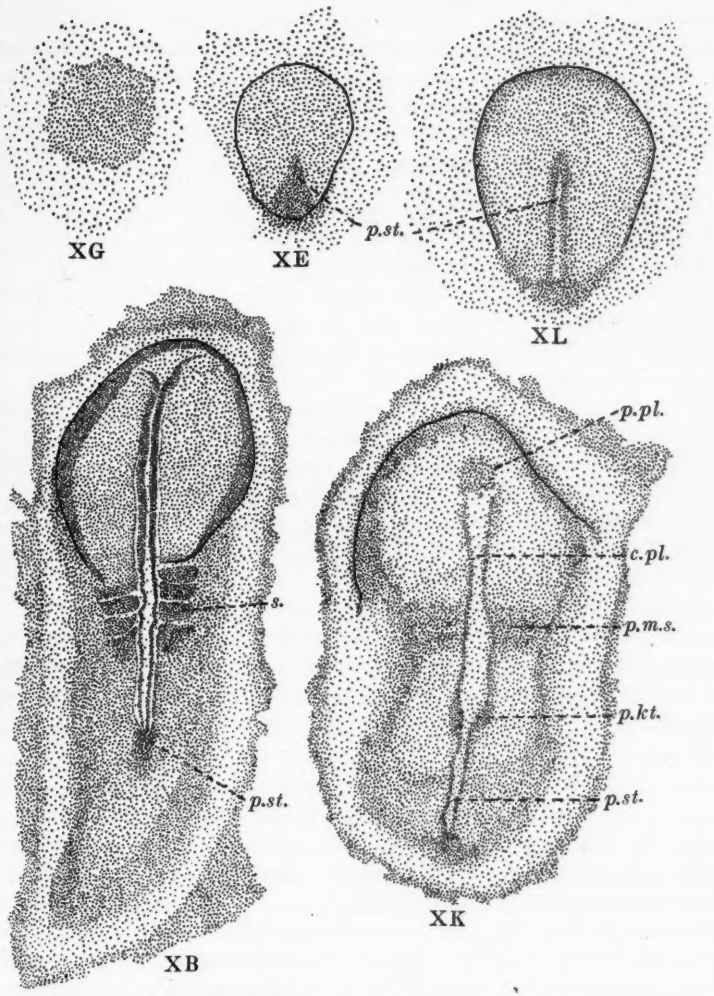


Fig. 1. Camera lucida drawings of embryonic areas at the stages of explantation (×26).

XG. Late pre-primitive streak.
XE. Stage of posterior thickening.
XL. Medium primitive streak.
XK. Pre-somite.
XB. Three somite.

p.st. primitive streak; *p.pl.* prochordal plate;
c.pl. chorda plate; *p.m.s.* pre-mesodermal somite;
p.kt. primitive knot; *s.* somites.

The results secured from the culture of each stage will be discussed separately. In general, the younger the stage explanted the less has been the development attained.

Table I includes the results obtained in the experiments. Unless so indicated all the cultures were grown upon clots composed of equal parts of adult chicken plasma and chick-embryo extract.

(*a*) *Late pre-primitive streak stage* (fig. 1, XG).

Cultures of this stage have been grown on the surface of plasma clots for as long as 5 days, during which time no visible differentiation could be distinguished either in the living culture or after fixation and staining. During the first 24 hours of culture the whole explant contracts or shrinks and becomes markedly thicker. The embryonic area becomes smaller, greatly thickened and rather irregular in outline. No outwandering of cells from the explant can be seen, nor has there occurred any noticeable liquefaction of the plasma.

In the succeeding days it becomes increasingly more difficult to distinguish the embryonic area from the trophoblast. After the third day the two cannot be distinguished and the whole explant appears as a very thick, dark mass of tissue of irregular outline. Outwandering of cells occurs very seldom. In several instances when the fixing fluid was poured into the watch-glass, the explant floated from the clot. This would indicate that the explant only survived, but made no use of the medium either as a source of food or as a supporting medium. Maximow considers that the failure of cultures of 6 days of age to differentiate was due to the destruction of the embryonic area by the invasion and phagocytic activity of the cells of the trophoblast. Whether this may be considered to be the case in the present experiment cannot be determined, as no sections have as yet been made of embryos explanted at this stage.

(*b*) *The stage of posterior thickening and elongation of the embryonic disc* (fig. 1, XE).

For the first 3 days the appearance of the explant is similar to that described above for the late pre-primitive streak stage, with the exception that outwandering of cells occurs about the second day. The embryonic area is still distinct on the third day, but has undergone considerable thickening, and its outline has become markedly irregular. Very little liquefaction of the plasma has occurred. This last is true of practically all the stages explanted. The outwandering of the trophoblastic cells indicates that the plasma is being used as a supporting medium. Moreover the food materials present in the embryo extract must be used, since the explant increases slightly in size. Some differentiation is apparent by the fourth or fifth day, when one or two pulsating vesicles may appear. Fig. 2 is a camera lucida outline drawing of a culture of 5 days' growth in which are seen two pulsating tubes widely separated by an irregular, very dark body of undetermined differentiation. Immediately above

the dark body is a clear, vesicular cavity, while below it the explant is thinner than around the periphery. These thin areas probably represent the former embryonic disc, and the thicker peripheral margin the trophoblast. The protocol of the experiment states that the embryonic area was more or less distinct on the fourth day, while on the second day there was a very short primitive streak.

In another example (Case XE6) the explant on the fourth day seemed everywhere of uniform thickness and condition except at one end where a single pulsating dumbbell-like body could be seen in association with a clear vesicle. As no further differentiation had occurred by the fifth day and as the heart was feebly beating, the culture was fixed.

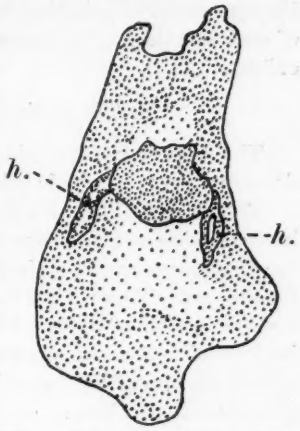


Fig. 2. Dorsal view of culture XE1. 5 days' cultivation. Camera lucida outline drawing (× 50). *h.* pulsating tubule.

Thus this stage possesses greater capacity than that of the late pre-primitive streak stage to maintain itself and to undergo differentiation, but its development is still markedly influenced by the very foreign environment. The chief increase in the differentiation exhibited is the occurrence of one or more pulsating vesicles or tubes.

(*c*) *The short primitive streak stage.*

A slight advance in the activity of the embryonic area is shown by this stage. In one example in particular the embryonic area, as well as the primitive streak, was markedly elongated at the end of the first day. The whole explant became increasingly more dense during the subsequent days until all distinction between embryonic area and trophoblast disappeared. After 48 hours in culture two widely spaced pulsating tubes were present at the extreme edges of the explant while, after 72 hours, these were increased to three. The third appeared also at the extreme edge, but almost between the other two. In no other culture of this or older stages have more than two pulsating tubes differentiated. No other differentiation occurred anywhere in the explant by the fifth day so the culture was killed. Other than the three "hearts" the culture appeared as a homogeneously thick, dark, flattened mass. It had practically doubled its size.

Another example, XA2, showed a marked elongation of the embryonic area and primitive streak. After 48 hours the latter was comparable to that of a long primitive streak stage. It was somewhat smaller than the control, while the embryonic area and trophoblast were very thick. Unfortunately degeneration occurred on the third day.

In comparison with the stage of posterior thickening a greater resistance

to environmental influences is shown by this stage. Noticeable are the elongation of the embryonic area and primitive streak after 24 hours of culture, and the appearance of pulsating vesicles on the second day. In explants of the stage of posterior thickening, pulsating vesicles appeared only after 4 or 5 days of culture.

(*d*) *The medium primitive streak stage* (fig. 1, XL).

The stage of medium primitive streak is the earliest stage from which these developed any embryonic primordia other than pulsating tubes.

Reference to Table I will show that a relatively small percentage of embryos develop and that these never develop very far. In most of the examples the phenomena occurring in the cultures are similar to those already described for the earlier stages. Thus there is a shrinkage and thickening of the explant, early elongation of the primitive streak and embryonic area, subsequent loss of individuality of embryonic area and trophoblast, and finally the appearance of one or two pulsating tubes in an otherwise thickened, more or less homogeneous mass of tissue.

Exceptions to this occurred in cultures XL2–XL4. Case XL2 gave rise after 48 hours' culture to a somewhat distorted but otherwise complete embryo with four pairs of somites. After 24 hours of culture the embryonic area as well as the primitive streak were markedly elongated and the stage was comparable to the control pre-somite stage. By the second day there had occurred a considerable advance in the degree of development; a typical three-part brain composed of prosencephalon, mesencephalon and myelencephalon was visible, as well as a short neural tube bordered by four pairs of somites, and there was a considerable thickening of tissue in the region of the tail. The initial appearance of the head fold separated the anterior tip of the head from the remainder of the embryonic area. A single elongated pulsating heart extended anteriorly to the head. The optic vesicles were indicated, and there was a short rod lying beneath the anterior end of the neural tube which was interpreted as the notochord. After 72 hours of culture the heart was no longer beating, and as visible necrosis was present in certain parts of the explant, it was killed.

Case XL2 was by far the best example obtained from explants of this stage. Case XL3 failed to show any differentiation other than a localised pulsation after 24 hours of culture. Cases XL and XL4 developed typical three-part brains, and short neural tubes, but only XL4 formed two hearts. Cases XA1 and XC1–XC4 gave no differentiation whatsoever, and appeared as thickened masses of tissue. In case XC5 two pulsating vesicles were visible on the third day of culture.

Cases XL2 and XL3 are especially interesting, as they were grown upon a medium composed of adult chicken plasma and rat-embryo extract. It cannot be said at this time that the high degree of differentiation present in case XL2 was the result of the rat-embryo extract. Reference to cases XK1 and XK3 below, in which the pre-somite stage was explanted to the same medium, show

Table I. *Summary of culture experiments.*

(Unless so indicated all cultures were grown in chicken plasma and chick-embryo extract.)

Cases	Comments	Days cultured 1	2	3	4	5
Late pre-primitive streak:						
XF6		Shrinkage and thickening	Shrinkage and thickening	Thick mass	No differentiation	
XF7		,,	Elongated mass		,,	
XF8		,,	,,		,,	
XG6		,,		,,	,,	
XG7		,,		,,	,,	
XG8		,,	Elongated mass		,,	
Posterior thickening and initial elongation:						
XE2		Disc distinct, shrinkage	Shrinkage and thickening		No differentiation	
XE5		,,	,,	Infected	,,	
XE6		,,	,,		1 heart	No further differentiation
XE1 (Fig. 2)		,,	,,		Elongation and thickening of disc	2 hearts, neural tissue?
Short primitive streak:						
XL1		Elongation of primitive streak, thickening	Thickening, 2 hearts	3 hearts, culture very dense	No further differentiation	No further differentiation
XA2		Elongation of disc	Pre-somite stage	Necrosis		
Medium primitive streak:						
XA1		No differentiation	No differentiation, changed to fresh medium	Necrosis		
XC1		Shrunken	Thickening	No differentiation	No differentiation	
XC2		Shrunken and thickened	Medullary plate?	,,	,,	
XC3–XC4		,,	Thickening	,,	,,	
XC5		Curled mass	Thick mass	2 hearts, medullary plate?	No further differentiation	
XC6	In refrigerator 12 hr.	Thickened mass		No differentiation	,,	
XC7	,,	,,	No differentiation	1 heart	,,	
XL2	Rat-embryo extract	Elongation of embryonic disc and primitive streak	4-somite embryo, 1 heart, brain, etc.	Fixed		
XL	Used as host for graft of portion of pr. st.	,, Also shrunken	Embryo with brain, neural tube, no beating hearts	Fixed		

Table I (*continued*)

Cases	Comments	Days cultured				
		1	2	3	4	5
XL3	Rat embryo extract	Differentiation obscure, thick mass, beating	No hearts	Fixed, no further differentiation		
XL4		Thickened mass	2 hearts, neural tube, cystic	2 hearts, brain	No further development	
Long primitive streak:						
XB4	Embryo very short	Embryo of 5 somites, medullary folds	Fixed			
XK4	Rat-embryo extract	Embryo of 6 somites, brain, tube, 2 hearts	Fixed			
32–198 (Fig. 4)		Brain, neural tube, ear vesicles	Fixed			
32–199 (Fig. 5)		Embryo of 5 somites	Fixed			
Pre-somite						
XD1		4 somite embryo, 2 hearts, brain	No change	Fixed		
XK1	Rat-embryo extract	8 somites, brain, no heart beat	No heart beat, fixed			
XK2		6 somites, brain	Heart beating, fixed			
XK3	Rat-embryo extract	5 somites, brain, 2 hearts	Fixed			
32–231 (Figs. 7, 8)		5 somites, brain, fixed				
Two somite:						
XB1		9 somite embryo	Appearance of membranes	Fixed		
XB2 (Fig. 6)		5 somite embryo	Fixed			
XB3	Cut transversely between somites A, anterior piece. P, posterior piece			A. Brain, hearts, neural tube, somites. B. Neural tube, somites		
XD2		8 somite embryo, 2 hearts, brain	Covering by membranes	Fixed		
XD4		9 somite embryo	,,	,,		
XD3	Cut transversely just anterior to somites. A, anterior; P, posterior		A. 2 hearts, brain. B. Neural tube, somites	,,		
XD12 (Fig. 3)	In refrigerator at 5° C. for 6 hours	6 somite embryo, fixed				

that the resulting embryos were certainly no better, and perhaps even worse, than others grown upon chick-embryo extract, and the same is true of case XK4, an explant of a long primitive streak stage. These experiments were tried for the purpose of finding a better growth-promoting medium. The most that can be said at the present time is that rat-embryo extract does not furnish obviously better growth-promoting factors for the rabbit embryo than does chick-embryo extract.

The effect of a lowering of temperature upon the development of these early stages is a question which is still unsettled. As was stated in the section on methods, all experiments were performed at room temperature and explantation made to the surface of a cold clot. In the case of the chick embryo, similar methods appear to have no effect upon the development of the explant, but it is well known that chick embryos can undergo lowering of incubation temperature, as, for instance, at the gastrula stage, with no apparent ill-effects. If for some reason the hen fails to deposit a fertilised egg and it remains in the uterus overnight, development continues, and at the time of laying the embryo usually is in the gastrula stage. If not incubated at once, the embryo may remain at this stage for a relatively long time, development continuing when the egg is incubated. The mammalian embryo is never subjected to such a change of temperature at any point in the course of its development, consequently at first sight it might be expected that such a change of temperature as occurred during these experiments would greatly influence subsequent development. To test this question further, portions of the uterus containing embryos in the medium primitive streak stage were placed in a refrigerator at 5° C. for 12 hours, after which the embryos were explanted. In case XC6 no differentiation occurred, and the culture resembled others of the same stage not similarly treated, in which no differentiation occurred. Case XC7 contained one pulsating tube after 72 hours of culture. Portions of a similar stage transplanted between the epiblast and endoderm of a chick blastoderm lived and became incorporated as grafts. A two-somite embryo (XD12), which had been in the refrigerator for 6 hours, developed after 24 hours into an embryo with six pairs of somites, brain, neural tube and notochord, which was quite similar to other explants which had not been treated in this manner (fig. 3). Moreover portions of two-somite stages subjected to this same lowering of temperature for 5–6 hours and subsequently transplanted to the chick blastoderm became incorporated as grafts and differentiated into somites and neural tube.

These experiments would seem to indicate that the mammalian embryo, at least in its earlier stages, may be subjected to considerable lowering of temperature without markedly affecting its development *in vitro* otherwise than by retarding it. It remains to be seen whether the maintenance of a constant body temperature will give more complete and further differentiation *in vitro*.

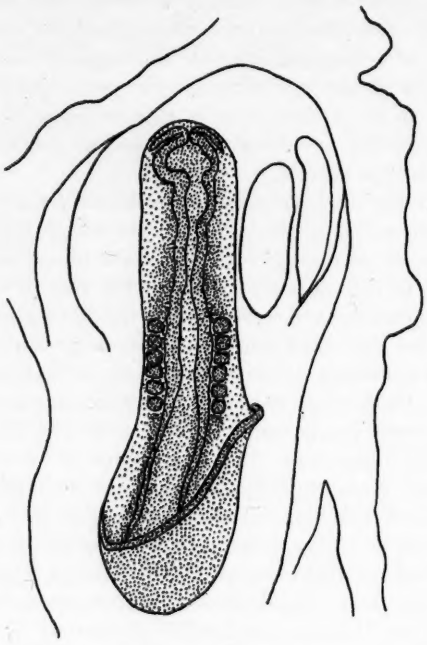


Fig. 3. Dorsal view of culture XD12. 24¾ hours' cultivation. Camera lucida outline drawing (× 33).

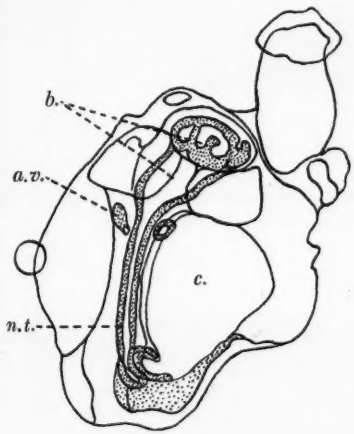
(e) The long primitive streak, pre-somite, and two or three somite stages (fig. 1, XK, XB).

In every case explants of the long primitive streak stage develop embryos with brain, neural tube, somites, one or two hearts, and possible notochord. Several of the better differentiated embryos are included in Table I. Maximum development is attained after 24–48 hours of culture and the embryos have usually been killed on the second day. No further differentiation occurs after this interval as far as can be seen from the observation of living cultures. The hearts cease to beat and centres of necrosis appear which gradually spread throughout the culture. Similar phenomena occur in cultures of the older stages. In fact explants of these three stages cannot be successfully cultivated longer than 48 hours.

Cases 198 and 199 (figs. 4, 5) are camera lucida outline drawings of explants of the long primitive streak stage which have been cultivated for 48 hours. In both instances a recognisable young embryo may be clearly seen; that in fig. 5 shows better differentiation than the other as regards the somites. A normal three-part brain, auditory vesicles, optic vesicles, five pairs of somites, neural

tube and head fold are present in fig. 5. In the living culture two beating heart primordia lay on either side of the embryo in the region of the mesencephalon. Considerable outwandering of cells was visible around the periphery of the culture. Efforts to subculture such stages after 48 hours have resulted in the death of the embryo. The embryonic tissues, especially the endoderm, adheres so firmly to the plasma that the embryo cannot be removed without injury. If greater technical skill will permit this, it is possible that the embryo may be kept alive for longer periods of time.

Another explant of the same stage (Case XK4) was grown upon a medium composed of adult chicken plasma and rat embryo extract. The degree of differentiation was similar to that just described above with the exception that six pairs of somites were visible. This difference is not great enough to be significant.



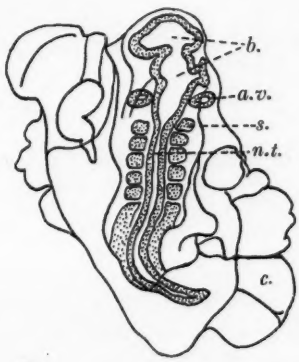


Fig. 4. Dorsal view of culture 32–198. 48 hours' cultivation. Camera lucida outline drawing (× 33). *b.*, brain; *n.t.*, neural tube; *a.v.*, auditory vesicle; *c.*, trophoblast.

Fig. 5. Dorsal view of culture 32–199. 48 hours' cultivation. Camera lucida outline drawing (× 33). *s.*, somite; other lettering as before.

It is interesting to note that explants of the pre-somite and two-somite stages fail to develop beyond that of the embryo just described. It might be expected that, considering the advanced degree of differentiation present at the time of explantation, more normal embryos might result. But this is not the case (cf. figs. 6, 7, 8). In some instances eight or even nine pairs of somites developed, but otherwise no difference could be seen in comparison with the embryos from the long primitive streak stage. The use of rat embryo extract likewise did not apparently affect development. In one example (XK1) the embryo contained eight pairs of somites, in another five pairs.

Apparently the development of the explants beyond that described above is

prohibited by the mechanical restrictions of the environment. The embryo develops in the form of a flattened sheet without the differentiation of body form, the feature of which in turn checks organ differentiation.

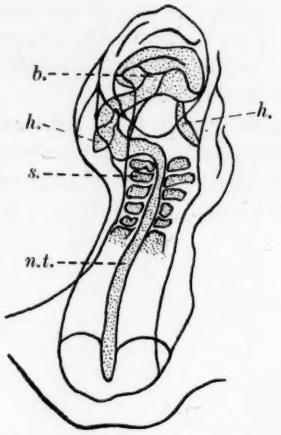


Fig. 6. Dorsal view of culture XB2, explanted in pre-somite stage. 29 hours cultivation. Camera lucida outline drawing (× 33). *h.*, heart, other lettering as before.

SUMMARY

1. The results of the present experiments show that young rabbit embryos may be grown *in vitro* upon a medium of adult chicken plasma plus a saline extract of chick-embryo extract and that considerable differentiation may occur.

2. A previous lowering of the temperature has no effect other than a slight slowing up upon this differentiation. Moreover rat-embryo extract may be substituted for that of the chick without affecting the results.

3. The older and more differentiated the embryo at the time of explantation, the greater is the differentiation exhibited by the culture.

(*a*) The stage of late pre-primitive streak gives no apparent differentiation as seen in whole mount preparations. Localised thickenings only occur.

(*b*) The stage of posterior thickening and initial elongation of the embryonic disc develops one or two beating hearts, and localised thickenings after 4–5 days' growth *in vitro*.

(*c*) The stage of short primitive streak undergoes marked elongation of the primitive streak and embryonic disc on the 2nd day; two, and in one case three, beating hearts appeared after 2–3 days of culture.

(*d*) The stage of medium primitive streak gives results comparable to (*c*). In several instances brain, hearts, neural tube and somites appear.

Fig. 8. Dorsal view of culture 32–231, after 24 hours' cultivation. Note optic vesicles, somites, folding of embryonic area and contraction of trophoblastic portions. (Approx. × 25.) Photograph.

Fig. 7. Dorsal view of culture 32–231, at time of explanting: late pre-somite stage. (Approx. × 30.) Photograph.

(*e*) The stage of long primitive streak gave rise to embryos with as many as six pairs of somites after 1 day of culture, and the pre-somite and two-somite stages give only slightly, if at all, better development.

4. Pulsating muscular tissue (? heart tissue) differentiates very easily from the earliest stages where no differentiation of any other primordia is noticeable.

5. The distortion present in most of the cultures is the result of the mechanical conditions, which greatly hinder the development of folds.

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THE GROWTH OF THE EPIPHYSES OF THE LONG BONES IN THE MADDER-FED PIG

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While there is general agreement that growth in length of long bones is mainly due to diaphysial activity, the subject of epiphysial growth has not been carefully investigated, and is well-nigh absent in the literature (1–6). With few exceptions the observations available are inadequately supported.

Testut (7), Poirier (8) and Franceries (9) state that the epiphyses grow in length by additions to their diaphysial surfaces.

Jamieson (10) states that the epiphyses grow by additions to both the diaphysial and articular surfaces.

Macewan (11) states that the epiphysial discs have nothing to do with epiphyses and suggests that they should be called diaphysial discs. Keith (12) confirms Macewan's statement. Goodsir (13) states that in a physiological sense an epiphysis should be regarded as a separate bone. Bergmann (14) states that the epiphyses grow on the side nearest the joint.

These various statements have been made from the direct study of the growing bones except the last (Bergmann), where radiographs of the long bones of a girl 5½ years old have been used.

The present contribution attempts to solve the problem whether the epiphyses grow by additions to their diaphysial surfaces, to their articular surfaces, or both.

MATERIALS AND METHODS

The observations and measurements are made from the epiphyses of the limb bones of madder-fed pigs used in my recent published investigation on diaphysial growth (15).

The epiphyses were derived from the limb bones of a dozen madder-fed pigs varying in age between 80 and 587 days.

In the case of an older animal whose rate of growth was diminishing in rapidity, the madder was withheld for a longer period before killing than in the case of the younger animals. They were thus treated by the "indirect madder method," whereby the new bone of the non-madder period shows up white against the background of the thoroughly maddered skeleton. Table I gives particulars of age, madder period, and growth period without madder.

The skeletons were macerated in a weak solution of KOH (0·1 per cent.).

Table I. *Duration in days with and without madder-feeding*

Pig No.	Age at death days	Madder period days	Non-madder period
14	80	72	8
15	91	77	14
16	108	84	24
17	126	105	21
12	140	61	28
1	169	68	29
2	197	97	28
3	225	125	28
4	279	153	54
6	362	207	84
9	475	271	126
8	587	394	116

PRELIMINARY OBSERVATIONS

All the epiphyses of the limb bones separated readily except in the case of the oldest animals, in which bony union of the distal humeral and proximal radial epiphyses was seen in No. 6 (362 days). No additional epiphyses had united in No. 9 (475 days). In the oldest pig, No. 8 (587 days), in addition to the above two the distal tibial epiphysis had also united. It has been possible to ascertain from the bones of older pigs, treated in the same way as this series, that at 647 days in addition to the foregoing, the proximal ulnar, femoral and distal fibular epiphyses have united. The remaining epiphyses—distal radial, ulnar, femoral; proximal humeral, tibial and fibular—have united in a pig aged 729 days.

Both Stevenson (16) and Dawson (17), the former working on human bones, the latter on those of the albino rat, agree that in general there is an age sequence of union of epiphyses. The sequence given by these workers is noted below and contrasted with the sequence of union of the epiphyses under present consideration (Table II).

Table II. *Sequence of union of epiphyses from the first to the last*

Present investigation in pig		Stevenson's results in Man	Dawson's results in albino rat
Distal humeral Proximal radial	362 days	Distal humeral Proximal radial	Distal humeral Proximal radial
Distal tibial	587 ,,	Proximal ulnar	Distal tibial
Proximal ulnar Proximal fibular Distal fibular	647 ,,	Proximal fibular Distal tibial Distal fibular	Distal fibular Proximal ulnar Proximal fibular
Distal radial Distal ulnar Distal fibular Proximal humeral Proximal tibial Proximal fibular	729 ,,	Proximal tibial Proximal fibular Distal fibular Distal radial Distal ulnar Proximal humeral	Distal fibular Proximal tibial Proximal fibular Distal radial Distal ulnar Proximal humeral

This latter sequence is necessarily very inadequate, as only a few individual pigs are considered as contrasted with the large number of skeletons examined

by Stevenson and Dawson. These workers point out that in the limb bones the distal humeral epiphysis is the first to unite and the proximal humeral epiphysis the last. In this series of pig bones the distal humeral epiphysis is one of the first to unite and the proximal humeral epiphysis is one of the last to unite.

Humphry (18) states that "the end of the shaft at which the epiphysis is last united is the end at which growth takes place most quickly." The following table (III) confirms this for the present series of pig bones. The ends of the diaphyses with greater and lesser increments have been described in my previous paper (15), and the results therein detailed are utilised in Table III.

Table III. *The relation of last uniting epiphysis to diaphysial end showing greatest increment*

In the case of the	Humerus	{ The last epiphysis to join the diaphysis is the			}	Proximal	{ The increment of this end of the diaphysis is the greater			
,,	,,	Radius	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Ulna	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Femur	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Tibia	,,	,,	,,	Proximal	,,	,,	,,	,,
,,	,,	Fibula	,,	,,	,,	Proximal	,,	,,	,,	,,

The general distribution of new bone of the epiphysial surfaces has already been observed (15). The articular surfaces of the epiphyses are covered by new bone. The contiguous surfaces of the diaphyses and epiphyses present a marked contrast—the ends of the diaphyses being entirely composed of new white bone, and the diaphysial surfaces of the epiphyses being red with no addition of new white bone even for the longest non-madder period.

The contiguous surfaces of epiphysis and diaphysis have reciprocal elevations and depressions which Thomson (19) has shown to be more pronounced in those animals which maintain the knee in a flexed position. In addition to being irregular the diaphysial surfaces of the epiphysis are everywhere covered by small pits which give an eroded appearance to the surface (Fig. 1). These erosions are familiar on the diaphyses and are referred to by Kölliker (20) and Sharpey-Schäfer (21) as the Foveolae of Howship, and are stated to appear wherever absorption is proceeding. It will be shown by measurement that, unless these erosions on the diaphysial surfaces of the epiphyses represent absorption, the increments of new white bone on the articular surfaces give an increase in length to the epiphyses in excess of the actual.

GROWTH IN LENGTH OF EPIPHYSES

Methods of measurement. The epiphyses of the humerus, radius and ulna were sectioned in the sagittal and those of the femur, tibia and fibula in the coronal planes (the same planes as used for the respective diaphyses).

A prominent ridge or depression on the diaphysial or articular surface of

each set of epiphyses was selected and the length (Table IV) was measured from this ridge or depression to the other surface in the long axis of the particular bone, as shown in Figs. 2–7.

Table IV. *Measurements of epiphyses in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	11·5	11·5	11·8	12·0	13·0	12·0	14·5	15·0	14·0	13·5	15·0	16·5
	Distal	12·5	13·0	13·0	13·5	14·0	13·5	14·5	16·0	16·0	14·5	15·0	17·0
Radius:	Proximal	7·0	7·5	6·0	7·0	9·0	8·5	9·0	9·0	9·5	9·0	8·5	9·0
	Distal	11·5	11·5	11·5	12·0	13·0	12·0	14·5	15·5	14·0	14·0	15·0	17·0
Ulna:	Proximal	14·0	13·0	13·5	15·0	17·0	16·0	18·0	19·5	18·5	19·0	17·5	18·0
	Distal	18·5	18·0	17·0	20·0	20·0	19·0	23·5	25·0	22·0	22·0	23·0	25·0
Femur:	Proximal	13·0	13·0	13·2	13·0	16·0	14·5	17·0	18·0	17·0	16·5	17·0	17·8
	Distal	18·5	18·5	17·0	19·0	21·5	19·5	23·8	26·5	25·5	26·0	28·3	31·7
Tibia:	Proximal	14·0	15·0	13·5	15·8	14·5	15·0	16·0	15·5	15·3	15·5	16·0	17·0
	Distal	8·4	8·0	8·0	8·0	8·5	8·0	8·8	9·0	8·0	7·8	8·5	10·0
Fibula:	Proximal	7·0	6·5	7·5	7·5	8·5	9·8	10·0	10·0	11·0	12·0	12·0	13·7
	Distal	12·0	12·0	12·0	12·8	13·5	13·5	14·5	14·5	13·0	13·0	13·5	16·4

This method of measurement was selected in preference to using an osteometric board, since the increment of new bone on the articular surface could be easily measured in the same line as the length (Figs. 2–7).

The proximal and distal epiphyses are unequal in length throughout the series; but, contrary to what one might expect, there appears to be no relation between the difference in epiphysial length and the ends of the diaphyses with the greater and lesser increments, e.g. the distal epiphyses of the humerus and fibula being longer than the proximal are adjacent to the ends of their respective diaphyses with the lesser increments.

The difference in length between the younger and the older epiphyses shows that, for each long bone, the epiphysis increases more at one end than the other. The epiphysis that increases most is situated adjacent to the diaphysial end with the larger growth (Table V).

Table V. *The association of greater epiphysial growth with the end of greater diaphysial growth*

		No. 14 mm.	No. 8 mm.	Difference mm.	Diaphysial end with greatest increment
Humerus:	Proximal	11·5	16·5	5·0	Proximal
	Distal	12·5	17·0	4·5	
Radius:	Proximal	7·0	9·0	2·0	Distal
	Distal	11·5	17·0	5·5	
Ulna:	Proximal	14·0	18·0	4·0	Distal
	Distal	18·5	25·0	6·5	
Femur:	Proximal	13·0	17·8	4·8	Distal
	Distal	18·5	31·7	13·2	
Tibia:	Proximal	14·0	17·0	3·0	Proximal
	Distal	8·4	10·0	1·6	
Fibula:	Proximal	7·0	13·7	6·7	Proximal
	Distal	12·0	16·4	4·4	

It will also be seen from Table V that the amount of growth over a period of (587 – 80) 507 days varies from 1·6 mm. in the case of the distal

Fig. 1. Photograph of the posterior half of the diaphysial surface of the proximal tibial epiphysis (Pig No. 6). To show the eroded appearance of this surface as described in text. Mag. × 3 approx.

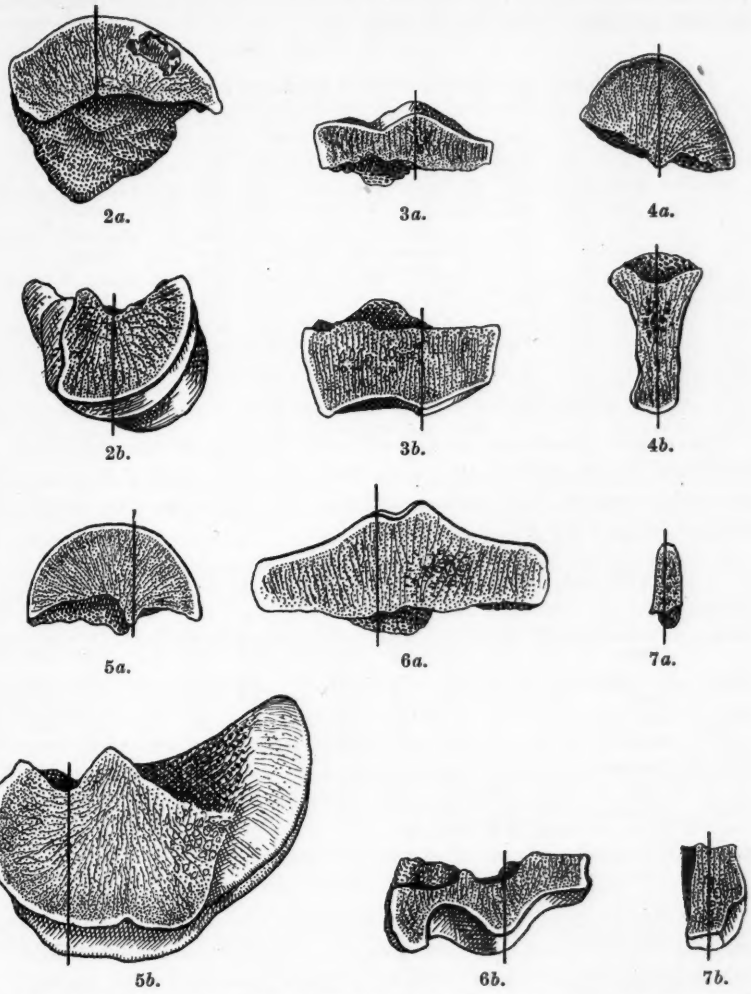

Fig. 2. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of humerus of pig 169 days old (No. 1).

In each of these figures (2–7) the areas of bone unstained by madder are represented white and indicate new bone laid down during the second non-madder period (29 days). Bone stained by madder is stippled. A vertical line indicates where the length of the epiphysis was measured as described in text.

Fig. 3. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of radius of same pig as Fig. 2.

Fig. 4. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of ulna of same pig as Fig. 2.

Fig. 5. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of femur of same pig as Fig. 2.

Fig. 6. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of tibia of same pig as Fig. 2.

Fig. 7. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of fibula of same pig as Fig. 2.

epiphysis of the tibia to 13·2 mm. for the distal epiphysis of the femur. These amounts are arranged in order in Table VI.

Table VI. *Extent of growth in various epiphyses for period of 507 days*

	mm.
Tibia, distal	1·6
Radius, proximal	2·0
Tibia, proximal	3·0
Ulna, proximal	4·0
Fibula, distal	4·4
Humerus, distal	4·5
Femur, proximal	4·8
Humerus, proximal	5·0
Radius, distal	5·5
Ulna, distal	6·5
Fibula, proximal	6·7
Femur, distal	13·2

MEASUREMENTS OF EPIPHYSIAL GROWTH

The growth increments at the articular ends of all the epiphyses, as represented by the layer of new white bone laid down during the respective non-madder periods, have been measured in the same axes as the length and are recorded in Table VII.

Table VII. *Measurements of new bone of epiphyses in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	1·2	1·8	1·7	1·5	1·5	1·0	1·2	1·0	1·3	1·0	2·0	2·0
	Distal	1·0	1·5	1·0	1·5	2·0	1·0	1·0	0·8	1·0	1·0	1·5	1·7
Radius:	Proximal	1·0	1·0	0·8	1·0	1·0	1·0	1·0	0·8	0·8	0·8	1·0	1·2
	Distal	1·0	1·0	0·8	1·0	1·5	1·0	0·8	1·0	1·0	1·0	2·5	1·8
Ulna:	Proximal	0·5	1·0	0·5	0·5	1·0	0·5	0·5	0·5	0·5	1·0	1·0	2·0
	Distal	1·0	1·0	1·0	1·0	1·0	1·0	1·0	1·0	0·5	0·5	2·0	2·0
Femur:	Proximal	1·0	1·5	1·0	1·4	1·8	1·0	1·0	1·3	1·0	1·5	1·5	1·0
	Distal	1·0	1·3	1·5	2·0	1·8	1·0	1·5	1·5	1·5	1·4	1·9	1·7
Tibia:	Proximal	1·0	2·0	1·5	1·5	2·0	1·8	1·5	1·5	1·0	1·5	2·0	1·5
	Distal	1·0	1·2	0·8	1·0	1·5	1·0	1·0	1·0	0·5	1·0	1·0	1·0
Fibula:	Proximal	1·0	1·0	1·0	1·3	1·6	1·5	1·0	1·0	1·0	1·5	1·8	1·8
	Distal	1·0	1·4	0·8	0·8	1·0	1·0	1·0	1·0	0·8	1·0	1·5	1·5

It is obvious from Table V that the growth increment is similar in the proximal and distal epiphyses, an interesting and also remarkable contrast to the unequal growth of the two ends of the diaphyses. Generally, the amount of growth in any epiphysis is rather less than that of the lesser growing end in any diaphysis.

GROWTH PER WEEK

Since the non-madder growth periods of the individual bones vary, having been increased with the age of the animal in order to obtain about the same amounts of new bone as the general rate of growth diminished, the growth increments cannot be directly compared. The table of measurements of new bone (Table VII) shows the increments during periods varying from 8 to

126 days. In order to compare rates of growth in young and old epiphyses, the amount of new bone laid down at the proximal and distal epiphyses has been calculated to one week (Table VIII).

Table VIII. *Calculated measurements of new bone in mm. per week during non-madder periods*

Pig No.	14	15	16	17	12	1	2	3	4	6	9	8
Humerus: Proximal	1·2	0·9	0·5	0·5	0·37	0·25	0·3	0·25	0·16	0·08	0·11	0·12
Distal	1·0	0·75	0·29	0·5	0·5	0·25	0·25	0·2	0·12	0·08	0·08	0·10
Radius: Proximal	1·0	0·5	0·23	0·33	0·25	0·25	0·25	0·2	0·10	0·06	0·05	0·07
Distal	1·0	0·5	0·23	0·33	0·37	0·25	0·2	0·25	0·12	0·08	0·14	0·11
Ulna: Proximal	0·5	0·5	0·14	0·15	0·25	0·12	0·12	0·12	0·06	0·08	0·05	0·12
Distal	1·0	0·5	0·29	0·33	0·25	0·25	0·25	0·25	0·06	0·04	0·11	0·12
Femur: Proximal	1·0	0·75	0·29	0·47	0·45	0·25	0·25	0·32	0·12	0·12	0·08	0·06
Distal	1·0	0·65	0·44	0·66	0·45	0·25	0·4	0·4	0·19	0·11	0·10	0·1
Tibia: Proximal	1·0	1·0	0·44	0·5	0·5	0·45	0·37	0·37	0·10	0·12	0·11	0·09
Distal	1·0	0·6	0·23	0·33	0·37	0·25	0·25	0·25	0·06	0·08	0·05	0·06
Fibula: Proximal	1·0	0·5	0·29	0·43	0·4	0·37	0·25	0·25	0·19	0·12	0·10	0·11
Distal	1·0	0·7	0·23	0·26	0·25	0·25	0·25	0·25	0·10	0·08	0·08	0·09

From Table VIII it is clear that there is a gradual diminution in the rate of growth in every epiphysis as one passes from the younger to the older epiphyses. The diminution is greater in the epiphyses which are adjacent to the end of the diaphysis with the lesser increment and which unite with the diaphysis first (Table III).

EXPECTED INCREMENTS OF NEW BONE

The rate of the epiphysial growth of the individual epiphyses now being known between 80 and 587 days, it is possible, taking the lengths of the youngest epiphyses as a starting-point, to calculate the growth increments that might be expected to be added at the stage of each successive older epiphysis. The differences in age of the successive older epiphyses do not always correspond to the non-madder growth periods, so that it is necessary to calculate from the rates of growth, the amount of growth for these periods of differences in age. The results of these calculations are set out in Table IX.

Table IX. *Measurements of new bone in mm. for periods of differences in age*

Pig No.	14	15	16	17	12	1	2	3	4	6	9	8
Humerus: Proximal	—	1·35	1·20	1·25	0·74	1·0	1·2	1·0	1·23	0·96	1·77	1·92
Distal	—	1·12	0·69	1·25	1·0	1·0	1·0	0·8	0·92	0·96	1·28	1·6
Radius: Proximal	—	0·75	0·55	0·82	0·50	1·0	1·0	0·8	0·77	0·72	0·81	1·12
Distal	—	0·75	0·55	0·82	0·74	1·0	0·8	1·0	0·92	0·96	0·99	1·76
Ulna: Proximal	—	0·75	0·53	0·37	0·50	0·48	0·48	0·48	0·46	0·96	0·81	1·92
Distal	—	0·75	0·69	0·82	0·50	1·0	1·0	1·0	0·46	0·48	1·7	1·72
Femur: Proximal	—	1·22	0·69	1·17	0·90	1·0	1·0	1·28	0·92	1·44	1·28	0·96
Distal	—	0·97	1·0	1·6	0·90	1·0	1·6	1·6	1·5	1·32	1·61	1·6
Tibia: Proximal	—	1·5	1·06	1·25	1·0	1·80	1·48	1·48	0·77	1·44	1·77	1·44
Distal	—	0·9	0·55	0·82	0·74	1·0	1·0	1·0	0·46	0·96	0·80	0·96
Fibula: Proximal	—	0·75	0·69	1·06	0·8	1·48	1·0	1·0	1·5	1·44	1·61	1·76
Distal	—	1·0	0·55	0·65	0·50	1·0	1·0	1·0	0·77	0·96	1·28	1·44

In Table X the differences in the actual length between the youngest and oldest epiphyses representing the actual amount of growth is compared with the expected amount of growth. This expected amount of growth is obtained from the summation of the successive increments of each successive older epiphysis shown in Table IX.

Table X. *The difference between actual and expected growth*

		Length No. 14 mm.	Length No. 8 mm.	Growth increase mm.	Expected increment mm.	Difference mm.
Humerus:	Proximal	11·5	16·5	5·0	13·62	8·62
	Distal	12·5	17·0	4·5	11·62	7·12
Radius:	Proximal	7·0	9·0	2·0	8·84	6·84
	Distal	11·5	17·0	5·5	10·29	4·79
Ulna:	Proximal	14·0	18·0	4·0	7·74	3·74
	Distal	18·5	25·0	6·5	10·12	3·62
Femur:	Proximal	13·0	17·8	4·8	11·86	7·06
	Distal	18·5	31·7	13·2	14·70	1·50
Tibia:	Proximal	14·0	17·0	3·0	14·99	11·99
	Distal	8·4	10·0	1·6	9·19	7·59
Fibula:	Proximal	7·0	13·7	6·7	13·09	6·39
	Distal	12·0	16·4	4·4	10·15	5·75

It is noted that the expected exceeds the actual increment to a varying amount of 11·99 mm. (proximal tibia) to 1·50 mm. (distal femur), the average excess being 6·25 mm.

It is remarkable that the comparison of the actual lengths of some of the youngest and oldest epiphyses shows a very small actual increase in length (distal tibia 1·6 mm., proximal radius 2·0 mm., proximal tibia 3·0 mm.) although the expected increments for these same epiphyses are 9·19, 8·84 and 14·99 mm. respectively, the last being actually the largest of the expected increments.

Now this excess of expected over actual increment presumably represents the amount of absorption which is occurring at the diaphysial surfaces of the epiphyses. Indeed the extent of absorption is almost as much as the increment.

The data provided by Table IX have been used to illustrate graphically the relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the epiphyses (Figs. 8–9).

SUMMARY AND CONCLUSIONS

This investigation of epiphyses of the madder-fed pig offers further confirmatory evidence that:

(1) The epiphyses grow at the side nearest the joint—Bergmann (14).

Attention is drawn to a new observation relating to the appearance of the diaphysial surfaces of the epiphyses indicating absorption.

This absorption is extensive and remarkable, because the expected exceeds the actual increment by an average of 6·25 mm., and because some of the epiphyses increase very little in length (distal tibia 1·6 mm., proximal radius

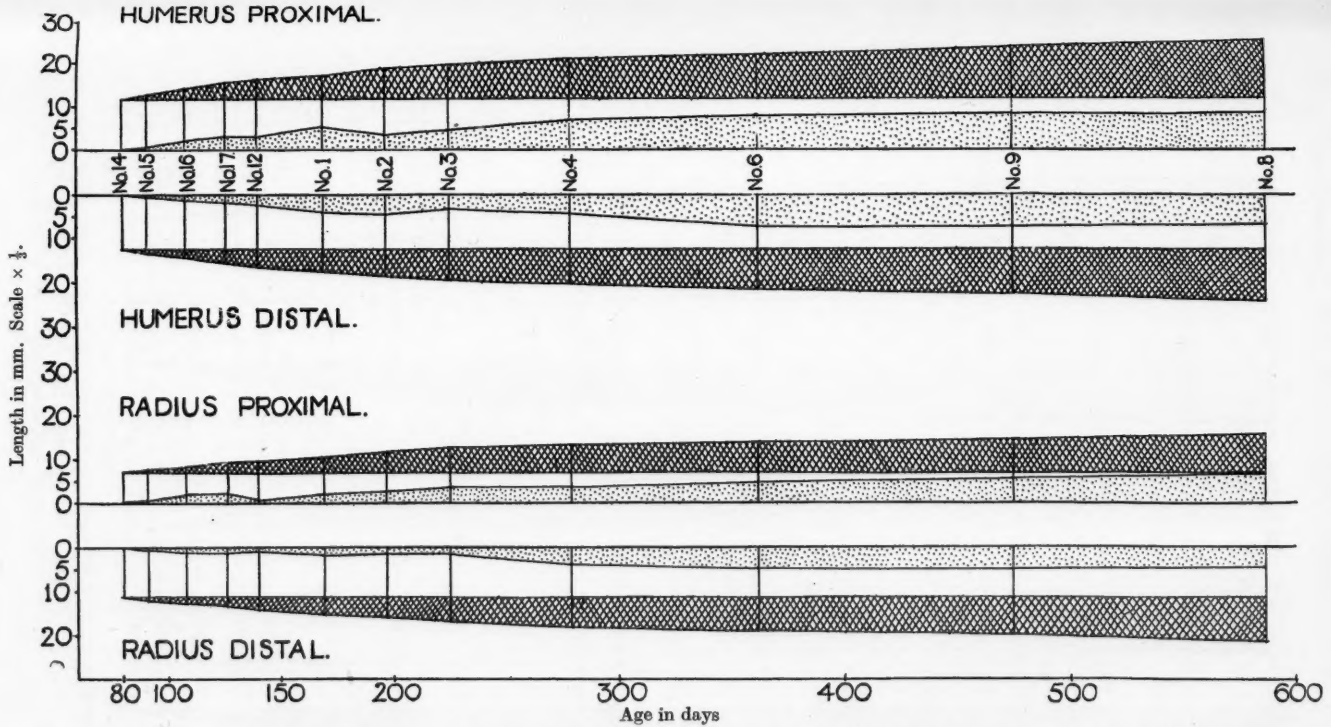

Fig. 8. Graphic representation of relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the humeral and radial epiphyses of madder-fed pigs as explained in text. The horizontal line represents 80–600 days on a scale of one day per 0·33 mm. The vertical scale represents length (scale natural). A vertical line cuts the horizontal base line at the age of each successive bone. The cross-shaded areas represent the observed increments of new growth. The actual length has been measured on the vertical lines representing age, so as to include the new growth, and the space between the actual and expected lengths has been stippled to represent the amount presumably absorbed. The actual length of each bone therefore includes cross-shaded and plain areas.

Fig. 9. Relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the femoral and tibial epiphyses of the madder-fed pig. Scales as in Fig. 8.

2·0 mm., proximal tibia 3·0 mm. in 507 days) although their rates of growth differ little from those epiphyses increasing as much as 13·2 mm. (distal femur) in the same period.

A method of graphic representation shows the relative amounts and rates of new bone added to the articular surfaces and of absorption from the diaphysial surfaces.

The actual measurements of the epiphyses show that, although the proximal and distal epiphyses are unequal in length, there is no relation between the difference in length and the ends of the diaphyses with the greater and lesser increments. The epiphysis of one end of each long bone increases more than that of the other. The one that increases most is situated adjacent to the diaphysial end with the larger growth. The amount of actual increase in length varies considerably from 1·6 mm. (proximal epiphysis of tibia) to 13·2 mm. (distal epiphysis of femur).

The amounts and quantitative ratios of new bone added to the articular surfaces of the epiphyses are demonstrated over given periods. The growth increment is seen to be similar in the proximal and distal epiphyses in contrast to the unequal growth of the two ends of the diaphyses.

Measurements of growth per week show that there is a gradual diminution in the rate of growth in every epiphysis as one passes from the younger to the older epiphyses.

(2) There is an age sequence of union of epiphyses as described by Stevenson (16) and Dawson (17).

(3) "The end of the shaft at which the epiphysis is last united is the end at which growth takes place most quickly"—Humphry (18).

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OBSERVATIONS ON THE VENAE CAVAE OF CERTAIN MAMMALS

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I. THE NORMAL LIE OF THE VENAE CAVAE, AND RELATED OBSERVATIONS

The normal lie of the venae cavae in the rabbit and in the cat has already been pictured in this *Journal* (1). That in three further species is now added. It should be noted that in all five the calibre of the abdominal vena cava as drawn may be slightly different from that in the living animal, as it is not visible in the X-ray photographs; also that the intrahepatic course of the vena cava was inserted by joining the point of entry into the liver to the point of emergence from the diaphragm. The actual intrahepatic course of the vein and its variations during the phases of respiration are to be recorded by X-ray cinematography combined with intravenous injection of "Abrodil" or of "Uroselectan," and will be reported later. For the X-ray photographs accompanying the present paper, I am indebted to the skill of Dr David Barnes.

The sheep (Plate I, fig. 3). A large lamb, with a snout-buttock length of 101 cm., was the subject. It was too large to screen, and was therefore photographed lying on its left side. Its resting respiration rate was 76 per min., its pulse rate could not be measured at rest, owing to its excitability. On 5 August, 1932, it was anaesthetised lying on its left side and, when it was deep under ether, the right side of the thorax was opened so that the movements of the heart, diaphragm, and thoracic inferior vena cava could be observed. The diaphragm contracted with *great* force and rapidity, and moved caudally and ventrally in so doing. The vein lengthened and became more horizontal (more in the long axis of the animal) as the diaphragm contracted—the X-ray shows rather the expiratory position. The amount of its lengthening was *c.* 25–30 mm. If inspiration was very forced, the heart was drawn caudally a little (6–12 mm.). The vein seemed to hang a little slack in the expiratory position, and to diminish in volume and calibre on strong inspiration, although it must be remembered in this connection that it lacked the normal sub-atmospheric inspiratory pressure outside it, and this would in the body tend to counteract the diminution in calibre due to lengthening. After these features had been noted, the animal was shot with the humane killer. The thoracic inferior vena cava, when taken *in situ* between the fingers and pulled, seemed to have a limit length beyond which it would not go. The X-ray photograph was completed in the usual way (1). In order to see if the abdominal vena cava had a

maximum distension point, as does that of the cat (3) and of the rabbit and the dog (2), a long glass tube was tied into it, and the vein was subjected to a pressure which rose gradually to 144 cm. H_2O. There was no appreciable increase in its diameter. The vein caudal to the renal vein entries had a double criss-cross arrangement visible even on superficial inspection; when examined more closely, this seemed to be composed of muscle fibres: internal to the muscle was a much less regularly arranged and rather thin collagen layer. The thoracic inferior vena cava was tied between two glass tubes and removed from the body. It showed elasticity and, after being stretched to its maximum (84 mm.), recoiled to 58 mm., a difference of 26 mm., corresponding very well with the lengthening observed on inspiration *in situ*. The lengthening was accompanied by a diminution in volume. Examination of the vein showed that it consisted of the following layers from without inwards. First, a collagen layer with no definite arrangement of fibres; this doubtless fixed the limit to which the vein could lengthen on inspiration without pulling the heart caudally. Next a longitudinal elastic layer, ensuing rapid shortening of the vein in expiration. Thirdly, a fine double criss-cross collagen spiral layer, allowing variations in length; the angle of intersection of the spirals was more acute on one side than on the other. Fourthly, the intima. In the superior vena cava there was no evident elasticity and no spiral arrangement of collagen fibres. The findings in this lamb are thus opposed to those previously reported in adult sheep (1), though these latter were checked by histology. One must provisionally, therefore, assume either variations with age or variations in individuals. Unfortunately, the size of the animals forbids the solution of the problem by X-ray screening.

The guinea-pig (Plate I, fig. 1). The thoracic inferior venae cavae from two guinea-pigs previously examined showed no elasticity or spirality of collagen fibres. It seemed improbable, therefore, that this vein in this species lengthened in inspiration. A female albino, weight 1120 g., with a snout-buttock length of 28 cm., pulse-rate 150 per min., and respiration rate *c.* 60 per min., was prepared for X-ray photography by being tied on a board with its fore-limbs pulled forward and its hind limbs pulled backward. The arch of the back in the photo is therefore less than the normal. On screening, one saw the heart shadow remain in its position in inspiration, while the diaphragm shadow moved caudally and ventrally, and the thoracic inferior vena cava apparently lengthened *c.* 6 mm. When the animal was killed and the thorax opened, the explanation was clear. The caval foramen, viewed from the side in the expiratory position of the diaphragm, was *c.* 5 mm. caudal to the anterior edge of the diaphragm. The muscle could, therefore, recede this distance in inspiration without any lengthening of the vein. On examination, the vein showed no elasticity or collagen spirality. On all counts, then, it would seem that this vein does not lengthen or move caudally in inspiration; it only becomes more horizontal. The slope of the vein down to the heart may be as much as 45° to the horizontal in expiration with the back strongly arched. Incidentally, this

particular animal had duplication of the vena cava posterior to the renal vein entries.

The dog (Plate I, fig. 2). The animal was first screened in a standing position. The heart shadow did not move caudally at all in inspiration, while the diaphragm shadow came up to the heart shadow in expiration, and moved caudally 20 to 25 mm. in ordinary inspiration, so that the thoracic inferior vena cava apparently lengthened in this phase of respiration. The photograph was taken with the dog lying on its left side. After it had been shot with the humane killer, details were added to the X-ray photograph in the usual way. There were slight discrepancies in the shape and position of certain organs as seen in the photograph and during dissection, so in the figure the X-ray appearance is marked in continuous white, and that visible on dissection by interrupted black lines. It is to be noted that in this species also the caval foramen of the diaphragm moves ventrally as well as caudally in inspiration, and the thoracic inferior vena cava hangs a little slack in the expiratory position.

In the normal standing position, then, the lie of the venae cavae in all five species so far investigated, and by presumption in all quadruped mammals, is such that there is an upward course of the inferior vena cava to the neighbourhood of the renal vein entries, and a downward course from there to the heart. The superior vena cava is short in the two species of rodents examined. The thoracic inferior vena cava lengthens on inspiration in the dog, rabbit and cat. It does not lengthen in the guinea-pig. The lengthening of the thoracic inferior vena cava on inspiration varies between 20 and 45 per cent., though the latter amount must be regarded as dyspnoeic.

II. THE SPIRAL ARRANGEMENT OF COLLAGEN FIBRES

In five species the movements of the thoracic inferior vena cava have been examined during life, and the structure of the vein investigated after death. All the results support the hypothesis that a spiral arrangement of collagen fibres occurs in this vein when it is normally subject to functional variations in length in the various phases of respiration. One is provisionally justified, therefore, in deducing that the vein lengthened in inspiration in the living animal when one finds such spirality of the collagen fibres post mortem. This is very valuable in the case of species which cannot readily be obtained alive for experimental purposes.

Another feature of importance recorded above is that the spirals in the dog's vein have a more acute angle of intersection on the ventral than on the dorsal side in the expiratory position of the vessel. The Sambur deer (1) had a vein similarly constructed, and one is probably justified in assuming that in inspiration this animal's vein lengthened more on the dorsal side than on the ventral, as this is what happened in the dog.

So post-mortem examination of the thoracic inferior cava of mammals may be used to deduce two points with regard to its activity during life.

With regard to other veins which also show collagen spirality (1), one may

provisionally accept the hypothesis that its presence allows functional changes in length, but this assumption must await final proof by X-ray cinematography combined with intravenous injection of "Abrodil" or of "Uroselectan".

The collagen spirals are very strong, e.g. the spiral collagen layer plus intima of a dog's thoracic inferior vena cava, though having a thickness when distended of the order of 20–30 μ, was able to withstand a pressure of 230 mm. Hg without marked deformation in shape. There is, however, a tendency for the volume of such a tube to increase with increase in pressure, so either the individual fibres must lengthen, or they must alter their positions relative to one another.

Incidentally, mercury inside a dissected vein is a good agent for showing up the spirals, and can be used thus to demonstrate them.

III. THE VOLUME OF THE THORACIC INFERIOR VENA CAVA OF THE DOG

A comparison of X-ray screen findings and of observations on the same animals with the right thorax open leads one to the conclusion that, with careful technique, one may assume the final relaxed position of the diaphragm with the thorax open to be approximately the same as the position in expiration in the intact animal. The "expiratory" length of the vein can, therefore, be measured after opening the thorax in this way, and will be either equal to, or just slightly greater than, the real expiratory length *in situ*; at all events it will not, with care, be less.

Experiments on the isolated thoracic inferior venae cavae from four different dogs showed that this vein had a maximum volume, under a moderate and approximately constant pressure, at its expiratory length and that the volume decreased very markedly when the vein was stretched to its inspiratory length, e.g. one vein decreased 56 per cent. in volume on being stretched to 140 per cent. of its expiratory length.

The results on dogs, therefore, are similar to those already recorded on cats and rabbits (3). Further experiments are now being made to see how the volume of this vein varies in the three species when the inspiratory decrease of intrathoracic pressure is simultaneously taken into account. The results of these studies will be reported later, together with measurements of the volume of the superior vena cava under corresponding pressures, and they will, it is hoped, give a quantitative estimate of the respiratory variations in volume of the intrathoracic venae cavae.

IV. THE DIAPHRAGM

A few brief notes only will be made about the diaphragm in addition to what has already been written. One is that its contraction in the dog and *par excellence* in the sheep, although very rapid in its execution, is more powerful than one would believe without seeing it, and even stretching the thoracic inferior cava to its inspiratory length requires quite a strong pull. The other is

that in the majority of dogs which have so far been examined, about fourteen, there was a band of muscle or tendon passing over the vena cava near its exit from the diaphragm. The inspiratory movements of the diaphragm have hitherto been too rapid for one to make any definite statement as to the action, if any, of the band on the vein, but it is possible that it may have some constricting action and, if a technique can be evolved, this further problem will also be investigated. Of the species which have been examined, the dog is least resistant to removal of the right thoracic wall, and the rabbit the most resistant. In at least one species, the cat, this production of an unilateral pneumothorax seems to result in a more powerful movement of the diaphragm.

SUMMARY

1. The normal lie of the venae cavae in three further species of mammals is pictured and described.

2. Further details are given about the spiral collagen structure of certain veins, and the importance of this structural peculiarity is discussed.

3. The volume changes of the excised thoracic inferior vena cava, which accompany changes in its length in the dog, are detailed.

4. Some miscellaneous observations on the venae cavae are included.

I wish to thank Mr G. K. Elphick for the ready assistance which he has given me on various occasions, Prof. I. de Burgh Daly for certain material. The results here described form part of a study of the venous return, the expenses of which are being defrayed by a generous grant from the Rockefeller Foundation.

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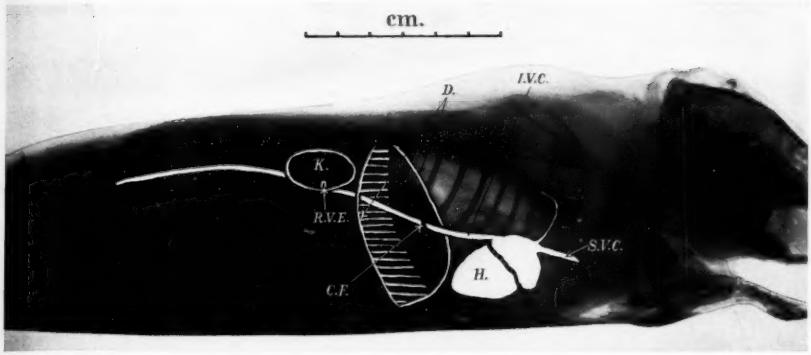
EXPLANATION OF PLATE

Fig. 1. X-ray photograph of guinea-pig in prone position with the fore-limbs pulled forward and the hind-limbs pulled backward. *H.* heart; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; *D.* diaphragm; *K.* kidney; *R.V.E.* renal vein entry; *C.F.* caval foramen in diaphragm. The shaded portion of the diaphragm is muscular, the unshaded tendinous.

Fig. 2. X-ray photograph of dog lying on its left side. *H.* heart; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; *D.* diaphragm; *K.* kidney; *R.V.* renal vein. Where the X-ray photograph differs from the appearance on dissection the former is in continuous white, the latter shown by dotted lines.

Fig. 3. X-ray photograph of large lamb lying on its left side. *H.* heart; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; *D.* diaphragm; *K.* kidney; *D.V.* diaphragmatic veins. The interrupted white line marks the junction of the muscular and tendinous portions of the diaphragm.



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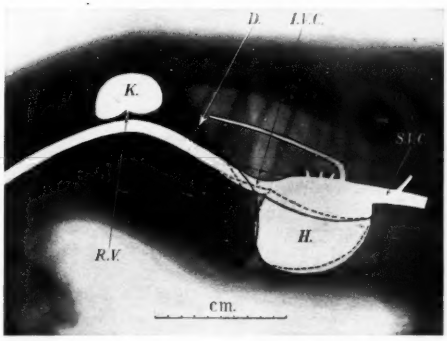

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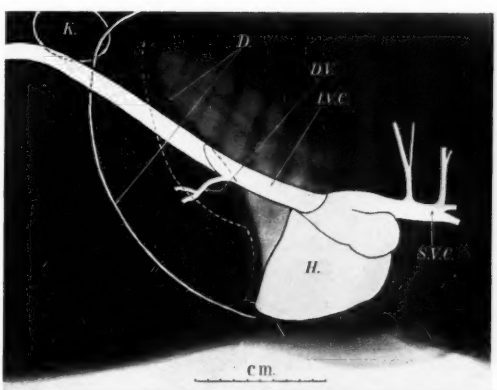

Fig. 3.

THE INVOLUTION OF THE TRANSITORY CORTEX OF THE MOUSE SUPRARENAL

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The cortex of the mouse suprarenal has two components: an outer part, showing no gross changes with age, which may be termed the permanent cortex; and a part immediately surrounding the medulla, histologically distinct from the permanent cortex, which is transitory. The transitory cortex has been studied in detail by two previous workers. Miller (1927), who termed it the *X* zone, found that it first became evident in both sexes at 14 days after birth. In males it had disappeared at 38 days; in females, however, it continued to grow, gradually disappearing by a fatty change, so that at 80 to 200 days glands from males and females were indistinguishable. Deanesly (1928) confirmed and supplemented the observations of Miller (1927), describing the development of a new cortical zone after the disappearance of the *X* zone.

In the present paper attention is confined to the involution of the *X* zone, the conclusions reached differing slightly from those of both Miller and Deanesly.

MATERIAL AND METHODS

Two hundred and thirty glands were taken from 119 mice of various colours, 58 males supplying 112 glands, 61 females supplying 118 glands. The ages of the mice ranged from 15 to 338 days. All glands were fixed in 5 per cent. potassium bichromate, to which an equal volume of 10 per cent. formol saline was added after 2 hours. After remaining in this mixture overnight, the glands were washed in water, dehydrated, cleared, and embedded in paraffin. Longitudinal sections were cut at 4 μ, and a ribbon containing the central sections mounted. They were stained with haemalum and eosin. Additional sections from some glands were stained by Weigert's stain for elastic tissue.

RESULTS

1. *The involution of the male* X *zone*

All glands at 15 to 17 days showed a healthy *X* zone. It was involuting in all at 28 days. In two pairs only a few *X* zone cells remained, and these were separated from the permanent cortex by a very thin sheet of fibrous tissue (fig. 1). The other two pairs of glands showed broader *X* zones, but signs of the separation of *X* zone from permanent cortex were obvious in each

of these four glands. In the glands studied the individual cells of the *X* zone appeared to be normal, no degenerative changes being seen in either nuclei or cytoplasm. At 57 days and at all the greater ages the male glands had the adult appearance. There was no trace of the *X* zone. The permanent cortex extended internally right up to the fine vascular fibrous tissue ensheathing the medulla, which had a perfectly smooth border (fig. 2).

2. *The involution of the female* X *zone*

At 15 to 17 days the female *X* zone was identical in appearance with that in the coeval male glands. Interdigitation of the *X* zone and medulla was more conspicuous than in males, but was not marked. At 28 days the *X* zone was broader than in the males, and no fibrous tissue could be seen separating *X* zone from permanent cortex. At 57 days two glands showed a few clear spaces. All the other glands at 57 and 85 to 86 days showed healthy *X* zones. At 111 to 112 days the *X* zone showed various phases of involution. One gland showed normal *X* zone on one side of the medulla, with interdigitation (fig. 3), whereas on the other side of the medulla in the corresponding situation there was an open network exactly like that seen in mature female glands from which the *X* zone has disappeared (fig. 4). The cells were fewer in number and the blood spaces wider than on the side where the *X* zone was normal. The edge of the medulla was smooth. The transition from normal *X* zone to the involuted area was quite gradual. The other gland of the pair showed the same features. A second pair of glands resembled this pair. A third pair of glands showed the *X* zone in an intermediate state. The *X* zone and medulla interdigitated slightly, and there was no fibrous band between them. The blood spaces were wider than in a normal *X* zone, and the nuclei of the *X* zone cells were smaller and stained more deeply. The last pair of glands showed a degenerate *X* zone outside a definite fibrous band. Within this a few healthy *X* zone cells were present. No evidence of involution by fatty change was found in this group of glands. At 141 days the *X* zone was absent. In one pair of glands a few small dark *X* zone cells could be seen lying between the fibrous band externally and the large dark cells of the medulla internally. At 167 days the *X* zone was absent from all; at 201 days, present in one pair; at 227 days, in one pair; at 252 days, in two pairs; at 280 days, in one pair; at 310 days, in one pair; at 336 to 338 days, in none.

3. *Basophilia of* X *zone cytoplasm* (*Miller*, 1927)

Miller (1927) found that the cytoplasm of the cells of the *X* zone stained definitely with haematoxylin after bichromate fixation. No definite haemalum staining of the cytoplasm of these cells was seen in any of the glands described above. Perhaps the result depends on the use of different methods of bichromate fixation. It is difficult to judge the colour of the cytoplasm because the strongly basophil nuclei of the *X* zone are so closely packed. Examined under a low power the whole *X* zone has a bluish tint.

DISCUSSION

1. *The involution of the* X *zone*

In the males the *X* zone had begun to involute at 28 days and had disappeared at 57 days. In the females, involution of the *X* zone was most frequent in the group at 111 to 112 days, an observation in fair agreement with that of Miller (1927), who found the highest incidence of degenerating *X* zones in a group whose age mid-point was 93 days. There is, however, a wide variation in the time at which the female *X* zone degenerates, and the factors on which this variation depends need elucidating. Miller (1927) noticed a similar variation, and suggested that it "might be lessened by breeding from one carefully standardized stock at one time."

The presence in single glands at 111 to 112 days of all stages from normal *X* zone to the fibrous band that replaces it in the adult, with no signs of the fatty change in the intermediate areas, indicates that the female *X* zone may sometimes degenerate without undergoing the fatty change as it does in the male. Involution without fatty change was observed by Miller (1927); and Deanesly (1928), who also saw both types, concluded that "in most glands studied, however, the *X* zone seems to disappear gradually as the result of an inconspicuous process of cell degeneration, which may begin either at the outside of the *X* zone or next the medulla." According to Deanesly's work and mine, therefore, involution of the female *X* zone without fatty change is the commoner mode.

In the males described above, the first sign that the *X* zone had begun to involute was the appearance of a very thin line of fibrous tissue between permanent cortex and *X* zone. This line became broader as the *X* zone cells disappeared, finally ensheathing the smooth-edged medulla of the adult gland. In the female, according to Miller (1927), "before or during the beginning of the degenerative process in the *X* zone, a regular connective-tissue line is laid down between the *X* zone and the rest of the cortex." This appearance was not seen in the glands described above, nor is it visible in any of Miller's (1927) figures illustrating the degenerative process. It can be seen, however, in the gland shown in Plate 14, Fig. 12, of Deanesly's paper. In her Fig. 13, "showing a later stage of degeneration of the *X* zone," there is no trace of such a connective-tissue line. It seems probable, therefore, that its occurrence is exceptional.

2. *The perimedullary fibrous band*

The appearances seen in the glands described above could be most simply explained by supposing that the perimedullary fibrous band replacing the *X* zone in the adult is formed, not by the deposition of new fibrous tissue outside the *X* zone, but by the shrinkage of the *X* zone stroma after the *X* zone cells have disintegrated. This would account for the occurrence of cells that I regard as *X* zone cells within the meshes of the uncontracted perimedullary

fibrous band in degenerating *X* zones. The congestion often seen would be due to dilatation of the pre-existing blood spaces owing to lack of the support that the *X* zone cells previously afforded. Deanesly (1928), who also believed that "a remnant of cells from the original *X* zone may persist among the fibrous tissue and outside it," stated that "during the resorption of the *X* zone the reticular fibrous tissue, which appears to be derived from the endothelium of the capillaries, proliferates and becomes more prominent." The evidence on which this conclusion was based was not produced.

Whether it is formed wholly by new fibrous tissue, wholly by old, or by both old and new, the perimedullary fibrous band remains, at least until 338 days, slightly broader in the female than in the male gland; hence Miller's (1927) statement that, after the *X* zone has disappeared, "the structure of the adrenal of the...female mouse is not different from the structure of the adult male gland" does not exclude this difference of degree.

3. *The time of complete involution*

When the *X* zone presents one of the various pictures of incomplete involution it is sometimes impossible to be certain whether cells with deeply staining nuclei adjoining the medulla are degenerate *X* zone cells or lipoid-free cells of the permanent cortex. A convenient rule would be to regard involution as complete when, in the absence of certainly recognisable *X* zone cells within the meshes of the perimedullary fibrous band, the inner edge of the perimedullary fibrous band is perfectly smooth. This rule would circumvent the difficulties due to the long persistence of small groups of *X* zone cells internal to the perimedullary fibrous band and to the appreciable variations in its width.

4. *Deanesly's "new cortical zone"*

Deanesly (1928) described the appearance of a "new cortical zone" after the disappearance of the *X* zone, based on the study of six female mice. The right gland was removed from each mouse four to seven weeks after the left gland. The glands from four of the mice are briefly described. The account of the "zona reticularis" of the left gland from mouse SCM. 11 corresponds exactly with the appearance of the inner part of the permanent cortex when free from lipoid. This "zona reticularis" was found to be larger in the right gland, and Deanesly stated that "the blood vessels and fibrous tissue next the medulla, however, appear to be extending into it, and it is probable that degeneration of the type found in the *X* zone is beginning." These glands were not illustrated; the evidence on which the conclusions were based was not produced; and the type of degeneration was not specified. The greater breadth of the "zona reticularis" may be due to decrease of cortical lipoid in the remaining gland after unilateral suprarenalectomy. This would be the simplest explanation of the appearances in the glands from mouse SCM. 4 also. Again, it was the right gland in which the "reticular zone" was well-marked, whereas in the left gland removed earlier "no definite inner zone" could be traced. It is stated that in the right gland "the fibrous reticular tissue round the

medulla has only penetrated the zone appreciably in one place." No evidence was adduced to support this statement. The site of what was thus assumed to be penetration seems to be illustrated in Deanesly's Fig. 6, where the low magnification does not allow details to be made out. It is significant that it occurs near one of the poles of the gland, and that, as stated in the corresponding legend, "the section lies to the outside of the median plane of the gland." This appearance, not rare in my own preparations, may result if the long axis of the gland is not parallel to the plane of section. The "zona reticularis" of the right gland of mouse SCM. 4 was "extensively vacuolated and hyperaemic." It was not illustrated. The "zona reticularis" of the right gland from mouse SCM. 15 "contains a number of degenerating cells." This gland is illustrated in Deanesly's Fig. 7, whose low magnification prevents appreciation of details. Paragraph (7) of the summary reads: "A new inner zone may arise later in the cortex; this though similar to the earlier one is distinguishable from it, but is also of a transitory character." No evidence was produced to show that it is transitory. The distinction between the two zones is, in my experience, simply that between *X* zone and permanent cortex which happens to be free from lipoid. In a later communication it will be shown that sudanophil lipoid occupies the whole or almost the whole permanent cortex while the *X* zone is present, in both sexes, and that when the *X* zone disappears, an increasingly broad zone round the medulla becomes lipoid-free. This general tendency to decrease of lipoid with age must be taken into account, along with the effects of unilateral suprarenalectomy on cortical lipoid in the remaining gland, a question reserved for detailed study. At present there is no convincing reason for regarding lipoid-free permanent cortex round the medulla as a zone with a distinctive character like that of the *X* zone.

5. *Identity of phase in each pair of glands*

For experimental purposes it is useful to know whether in each of a pair of glands the *X* zone is in the same phase. Miller (1927) found that both glands from a single mouse were in the same phase. Deanesly (1928) confirmed Miller's observation. All the glands in my series were examined to check this, and without exception each pair of glands showed the *X* zone in the same condition. This does not mean that throughout a single gland the *X* zone had reached the same stage of involution. As shown above, the *X* zone may exhibit different degrees of involution in different parts of the same gland; in this event, however, the same stages are visible in the *X* zone of the other gland from the same mouse. The *X* zone is usually of the same width in both glands from the same animal.

SUMMARY

1. No evidence that the cytoplasm of the cells of the *X* zone of the mouse suprarenal is basophil was obtained.

2. It is shown that the female *X* zone may involute without fatty change.

3. Deanesly's (1928) observation that involution by fatty change appears to be the less frequent mode is confirmed.

4. It is suggested that the perimedullary fibrous band that succeeds the *X* zone may be formed by collapse of the *X* zone stroma.

5. Until 338 days at least, the perimedullary fibrous band is appreciably broader in the female than in the male gland.

6. The observations here discussed lend no support to Deanesly's (1928) view that a second transitory zone succeeds the *X* zone.

7. It is suggested that the appearances taken to indicate a new zone are identical with those of permanent cortex whence lipoid has disappeared.

8. The observations of Miller (1927) and Deanesly (1928) that the *X* zone is in the same phase in both glands from one mouse are confirmed.

9. When the *X* zone is in various stages of involution in one and the same gland, the same stages are visible in its fellow.

10. The *X* zone is usually of the same width in both glands from one mouse.

I am indebted to Prof. S. L. Baker for counsel and criticism, and to Prof. J. S. B. Stopford for his interest in the work.

EXPLANATION OF PLATE I

Fig. 1. Early stage of involution of male *X* zone. Upper half of figure shows cortex; lower half, medulla. Between permanent cortex and medulla, the *X* zone is visible as a band of cells about five cells broad, staining rather more darkly than the permanent cortex. The nuclei are more closely packed in the *X* zone than in the permanent cortex. Separating *X* zone from permanent cortex are a few fibrous tissue cells with elongated nuclei parallel to the gland capsule. The edge of the medulla is irregular, its cells interdigitating with those of the *X* zone. From a male aged 28 days, H. and E. after bichromate. × 200.

Fig. 2. Adult male suprarenal. Upper left of figure shows permanent cortex; lower right, medulla, dark after bichromate. There is no trace of the *X* zone. The edge of the medulla is perfectly even, as in all adult glands. The thin band of cells immediately adjoining medulla is permanent cortex cells free from lipoid. They should not be mistaken for *X* zone cells. From a male aged 57 days. H. and E. × 200.

Fig. 3. The broad dark zone crossing the figure from top right to bottom left is a healthy *X* zone. Top left shows permanent cortex, staining more lightly. Bottom right shows darkly stained cells of medulla, which interdigitate with the cells of the *X* zone. From a female aged 111 to 112 days. H. and E. after bichromate. × 200.

Fig. 4. Another part of same gland as that shown in Fig. 3. Top left, cortex; bottom right, medulla, with the smooth border characteristic of maturity. Adjoining medulla, in the centre of the figure, is a cortical area containing many blood spaces. The *X* zone cells have disappeared. Involution is thus complete, but the shrinkage of the framework of the *X* zone that results in the formation of the perimedullary fibrous band has not yet occurred. H. and E. × 200.

Photographs by H. C. Taylor.

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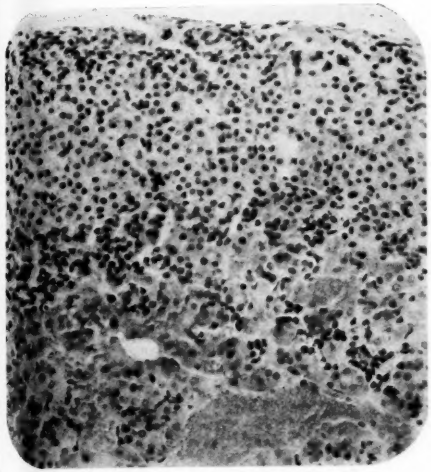

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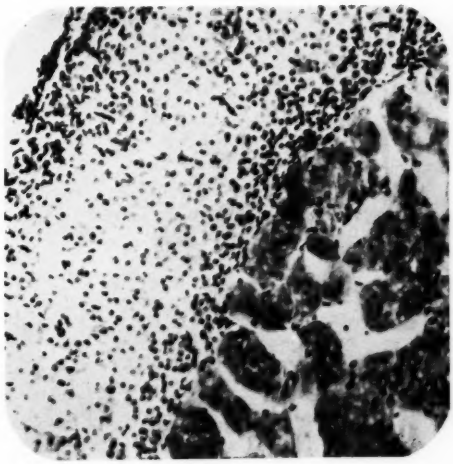

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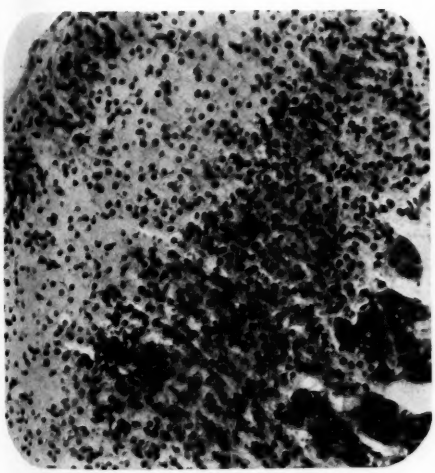

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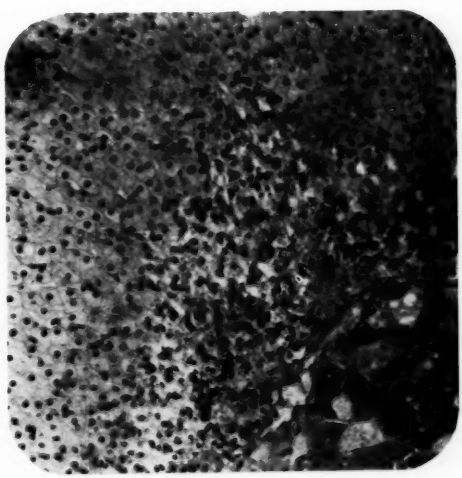

Fig. 4.

VARIATIONS IN THE CORTICAL LIPOID OF THE MOUSE SUPRARENAL WITH SEX AND AGE

By RAYMOND WHITEHEAD

From the Department of Pathology, Victoria University of Manchester

Whitehead (1931) found that lipoid was relatively more abundant in the cortex of female than of male mice, aged about 150 days. In the present paper it is shown that the amount of sudanophil lipoid in the mouse suprarenal cortex is most abundant, in both sexes, while the transitory cortex (*X* zone) is present.

MATERIAL AND METHODS

Two hundred and forty-seven glands were taken from 124 mice of various colours, 64 males supplying 127 glands, 60 females supplying 120 glands. The ages of the mice ranged from 15 to 338 days. The age groups in this series are the same as those in the series discussed by Whitehead (1933). All the glands were fixed in 10 per cent. formol saline, cut frozen, stained with haemalum and Sudan III, and mounted in glycerine jelly.

Method of measuring lipoid

The term "lipoid band" is used to denote that part of the permanent cortex whose lipoid-rich cells stain with Sudan III. The fat of the involuting *X* zone is thus excluded by definition from the measurements. The breadth of the lipoid band was measured with a micrometer at one point in a central longitudinal section. Such a section is roughly ovoid, with a blunt end and a sharp end, from which the central vein emerges. If these are termed the paravenous and venous poles respectively, an imaginary straight line joining them may be termed the major axis, and an imaginary straight line intersecting this axis at right angles midway between the poles may be termed the minor axis.

The measurements were made as a rule near the minor axis as here the cortex varies less in thickness over unit distance than near the poles.

The reading on each gland contained, from left to right, the breadth in micrometer units of: (*a*) capsule; (*b*) lipoid-free cortex outside lipoid band; (*c*) lipoid band; (*d*) lipoid-free cortex inside lipoid band; (*e*) perimedullary fibrous band together with *X* zone when present.

Specimen reading:

a	*b*	*c*	*d*	*e*
1	3	17	4	9

From these figures, the lipoid band occupied 0·5 of the width of the total cortex, 0·7 of that of the permanent cortex. Permanent cortex was measured

from the outer margin of the gland capsule to the outer margin of the *X* zone and/or perimedullary fibrous band.

Sources of error

The lipoid band is usually of uniform width and density, and it is easy to judge its limits. A systematic error is possible owing to the personal factor. The section was always illuminated by electric light, no filters being used. In a few glands the irregular distribution of lipoid prohibited measurement. In frozen sections it may be impossible to locate with certainty the junction between *X* zone and/or perimedullary fibrous band and lipoid-free permanent cortex inside the lipoid band.

THE RATIO OF LIPOID TO PERMANENT CORTEX (L./P.C.)

The values of L./P.C. are shown in Table I.

P.C. is taken as ten units to avoid a cipher and decimal point before each entry. Each entry represents one gland. For each age group of each sex there are two rows of figures. Those in the top row represent left glands, those in the bottom row the corresponding right glands. The average breadth of the lipoid band in all the glands of each group is given to the right of the individual values.

Table II, constructed from Table I, shows the difference between the values of L./P.C. in pairs of glands.

Table II contains three blocks of figures, the first for males, the second for females, and the third for both sexes together. The first column of each block states the number of pairs of glands in which the values of L./P.C. differed by the amount stated in the units column. The second column of each block contains the reduction to percentages of the figures in the first column.

Table II shows that in 84 per cent. of pairs the values of L./P.C. were either identical or differed by only one unit, and that the difference exceeded two units in only 8 per cent. of pairs, i.e. the breadth of the lipoid band usually bears the same proportion to the breadth of the permanent cortex in both glands from one mouse.

The results in Table I are shown graphically in figs. 1 and 2 for males and females respectively. Ordinates represent permanent cortex, taken as ten units. Abscissae represent age of mice in months. Each small square indicates one suprarenal gland. Where the ratio of the cortical lipoid band to permanent cortex is the same in two or more glands from mice of the same age group, the number of glands is indicated by the size of the rectangular areas. The bases of these areas mark the number of units of permanent cortex occupied by lipoid.

Fig. 1 shows that during the first month lipoid almost entirely fills the permanent cortex in males. From two months onwards the amount of lipoid

is more variable, and the range of variation tends to increase with age. The average amount of lipoid oscillates between five and seven units, showing no tendency to increase or decrease.

Table I. *Ratios of cortical lipoid band to permanent cortex (L./P.C.) in normal mouse suprarenal. P.C. is taken as ten units*

Age (days)	Males						Av.	Females					Av.
15–17	10	8	10	8	10		10	10	9	10	10	9	10
	10	10	10	—	10			10	9	10	10	10	
28	9	8	9	9	8	8	8	10	10	10	10	10	10
	9	9	7	9	8	7		10	10	10	10	10	
57	5	5	8				6	9	9	10	7	6	8
	5	5	8					9	10	10	7	7	
85–86	4	7	5	8	7		6	10	10	5			9
	6	6	5	8	8			10	7	10			
111–112	7	1	7	6			5	10	10	8			10
	7	1	7	6				10	10	10			
141	3	6	7	9	5		6	10	10	10	10	10	10
	2	8	7	8	8			10	10	10	10	10	
167	8	5	8	7	8		7	9	9	8	9	10	9
	6	3	7	8	7			9	9	8	9	10	
201	3	7	6				5	9	9	1	9		7
	2	7	6					7	8	2	9		
227	9	9	5	7	5		7	7	7	8	8	9	8
	6	8	6	6	6			8	7	8	9	8	
256	2	7	7	6	9		6	6	8	9	8	8	8*
	2	7	7	8	9			7	8	6	9	7	
280	2	8	5	4	5		5	7	5	1	8	8	6
	3	8	6	7	6			8	9	1	7	8	
310	7	10	7	9	2		7	5	7	8	7		7
	8	9	8	8	2			5	8	8	9		
336	5	6	9	5			6	10	8	9	8	1	7†
	4	7	9	6				10	9	8	7	1	
						Average	6·5					Average	8·4

* 252 days. † 336–338 days.

Table II. *Difference between values of L./P.C. in pairs of glands*

Units of difference	Males		Females		Males and females	
	Number	%	Number	%	Number	%
0	25	42	35	59	60	50
1	24	41	17	29	41	34
2	7	12	3	5	10	8
3	3	5	2	3	5	4
4	0	0	1	2	1	2
5	0	0	1	2	1	2
Totals	59	100	59	100	118	100

Fig. 2 shows that in females lipoid usually occupies the whole of the permanent cortex during the first five months of postnatal life. From six months onwards, the average amount of lipoid, though slightly higher than in males, tends to fall and extreme low values occur. The scatter, however, is not so great as in the males.

HISTOLOGICAL TYPES OF LIPOID DISTRIBUTION

For descriptive purposes three groups of glands may be recognised:

(1) Glands with a broad lipoid band, occupying not less than half the width of the permanent cortex (fig. 3).

(2) Glands with a narrow lipoid band, occupying less than half the width of the permanent cortex (figs. 4 and 5).

(3) Glands in which the lipoid is irregular (fig. 6).

Each group contains glands from both sexes. As figs. 1 and 2 indicate, Group I is much the largest.

Frequency of lipoid-rich subcapsular rim of cells

The subcapsular rim of cells ("glomerular" zone) is usually lipoid-free in both sexes. In the 110 measured glands from mice, aged 201 days and over (55 male and 55 female), lipoid extended right to the inner border of the gland capsule in 36 (16 male and 20 female), i.e. 33 per cent.

Site of lipoid variation

The histological results demonstrate that lipoid is most variable in the inner part of the cortex and least so in the layer of the cells below the subcapsular layer. Wolff (1927) made the same observation.

DISCUSSION

Relation of lipoid to X *zone*

In the paraffin-embedded glands from 119 mice of the same batch and age groups as those described above, it was found that the *X* zone had disappeared from males at two months, and was present in females only occasionally from five months onwards (Whitehead, 1932 *b*). The measurements reported in the present paper indicate that sudanophil cortical lipoid is most abundant and least variable in amount while the *X* zone is present. This is true of the suprarenals of both sexes, but owing to the longer persistence of the *X* zone in females, lipoid is relatively more abundant in females than in males during the interval between the disappearance of the male *X* zone and the disappearance of the female *X* zone. This must be remembered in interpreting lipoid changes in mice from about two to about five months of age.

When the *X* zone has disappeared from both males and females there is no definite evidence of a sex distinction in the amount and range of variation of sudanophil cortical lipoid. The lipoid phenomena shown by the female from five months onwards are similar to those shown by the male from two months onwards.

The extreme low values of L./P.C.

In seven of the males and three of the females whose measurements are given in Table I the ratio of L./P.C. was under four in one or both suprarenals. It was thought that this might have been the result of spontaneous disease.

In six of the males no macroscopic lesion was found. In the seventh, *cysticercus fasciolaris* was present in the liver. In the other two males presenting this abnormality the values of L./P.C. were the highest found in their respective age groups: 9 and 8, and 9 and 9. Therefore *cysticercus fasciolaris* cannot be the cause of the low value of L./P.C. in the male referred to.

One of the females was pregnant with six foetuses and had *cysticercus fasciolaris* in the liver. In the other two no abnormality was found.

Four males and four females showed irregularly distributed lipoid. One of the females was pregnant with two foetuses. The other seven animals showed no abnormality.

One female had a caseous inguinal gland. The ratio L./P.C. was 8 and 8, or one unit above the average for the age group.

From observation of only two pregnant females it is of course impossible to draw any conclusion. The low values of L./P.C. and of irregularly distributed lipoid cannot be attributed to the pregnancy.

Spindle cells, apparently identical with those described by Löwenthal (1931), were conspicuous in 26 out of the 230 paraffin-embedded control glands (Whitehead, 1932). These cells indicate inflammation of mild degree. It is possible that such inflammation was present in some of the glands used for lipoid measurements. There is, however, nothing in the literature of the suprarenal to justify the attribution of the low values of L./P.C. to inflammation of such low degree. The evidence points rather to increase of lipoid in mild intoxications (Deanesly, 1931). Since it is only severe and rapidly fatal infections that appear to be followed by a marked reduction or disappearance of lipoid, no pathological explanation can be offered of the low values of L./P.C. in eight mice, nor of the irregular distribution of lipoid in seven mice, all of which were clinically healthy and showed no lesions at autopsy. There seems to be no good reason for not accepting the low values of L./P.C. as physiological.

SUMMARY

1. It is shown that in both sexes sudanophil lipoid occupies almost the whole width of the permanent cortex while the *X* zone is present, in males up to one to two months, in females up to about five months.

2. When the *X* zone has disappeared the average amount of lipoid falls, and the amount of lipoid present in glands from mice of the same age group is more variable.

3. During the interval between the disappearance of the male *X* zone and of the female *X* zone, i.e. from about two to about five months of age, lipoid is relatively more abundant in the female than in the male gland.

4. Lipoid is usually present in the same amount and situation in both glands from one mouse.

5. Lipoid varies most in the inner part of the permanent cortex.

6. In one-third of the glands lipoid extended to the gland capsule.

I am indebted to Prof. S. L. Baker for counsel and criticism and to Prof. J. S. B. Stopford for his interest in the work.

EXPLANATION OF PLATE I

Fig. 1. Ratios of cortical lipoid band to permanent cortex in normal male mice. Ordinates: permanent cortex (ten units); abscissae: age in months. For details, see text.

Fig. 2. Ratios of cortical lipoid band to permanent cortex in normal female mice. Ordinates: permanent cortex (ten units); abscissae: age in months. For details, see text.

Fig. 3. The entire cortex is occupied by lipoid, stained dark by Sudan III. The fibrous capsule and the medulla appear light. The edge of the medulla is smooth, as in all adult mice. From a male aged 201 days. × 80.

Fig. 4. Sudanophil lipoid forms a narrow dark strip in the outer part of the cortex. The rest of the cortex appears lighter than the medulla. From a female aged 201 days. × 30.

Fig. 5. From the same gland as fig. 4, showing a narrow strip of lipoid-free cortex between lipoid band and capsule. The edge of the medulla is smooth. × 80.

Fig. 6. The sudanophil lipoid is irregularly distributed. It is most irregular in the inner part of the cortex. Lipoid reaches the capsule at a few points. From a male aged 141 days. × 60.

Photographs by H. C. Taylor.

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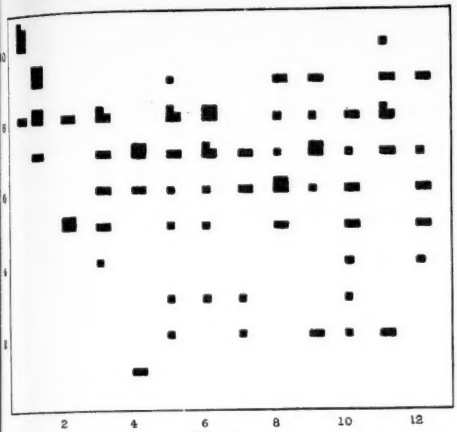

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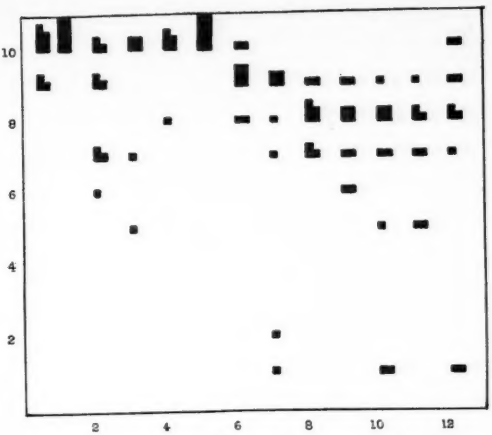

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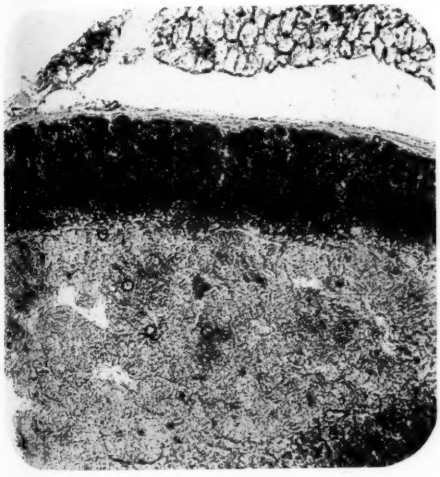

Fig. 3.

Fig. 4.

Fig. 5.

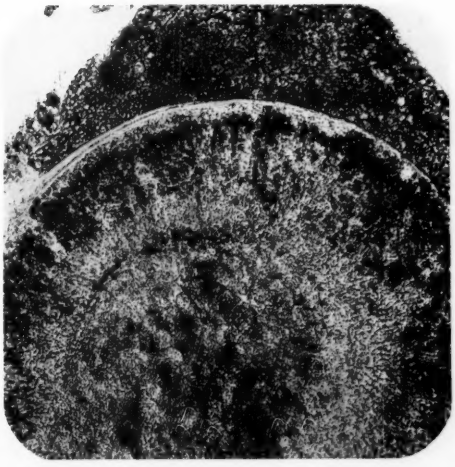

Fig. 6.

GROWTH AND MITOSIS IN THE MOUSE SUPRARENAL

By RAYMOND WHITEHEAD

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PART I. GROWTH

The following measurements were made to determine approximately the rate of growth of the cortex and medulla of the mouse suprarenal, and to provide a rough standard for judging whether glands from experimental animals are broader or narrower than the normal.

Material

The suprarenals from mice of various colours were fixed in 5 per cent. potassium bichromate, to which an equal volume of 10 per cent. formol saline was added after about 2 hours. After remaining in this mixture overnight the glands were washed in water, dehydrated, cleared, and embedded in paraffin. Longitudinal sections were cut at 4μ, and a ribbon containing the central sections mounted. They were stained with haemalum and eosin. Measurements were made of 106 glands from 57 males, and of 113 glands from 61 females.

Method of measurement

A central longitudinal section of the mouse suprarenal is roughly ovoid, with a rounded end and a pointed end, from which the central vein emerges. In a previous paper (Whitehead, 1933) these were designated the paravenous and venous poles respectively. An imaginary straight line joining them was termed the major axis, and an imaginary straight line intersecting this axis at right angles midway between the poles was termed the minor axis. Three sections of each gland were measured along the minor axis. Thus the breadth of the cortex was found by averaging six measurements, that of the medulla by averaging three.

Results

Explanation of figures

The results of the measurements are shown in four uniform figures. Ordinates denote breadths in mm.; abscissae, age of the mice in months. In figs. 1 and 2 each square denotes breadth of permanent cortex in one gland; in figs. 3 and 4 each square denotes breadth of medulla in one gland. Where two or more glands from mice of the same age group gave the same measurements the number of glands is indicated by the area of symmetrical rectangular blocks.

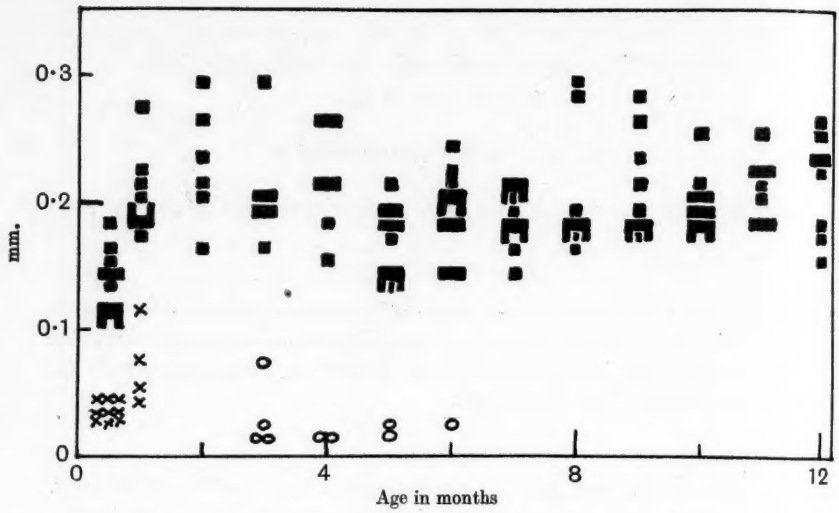

Fig. 1. Breadth of suprarenal cortex in male mice. Permanent cortex: squares; transitory cortex: crosses; perimedullary fibrous band: circles.

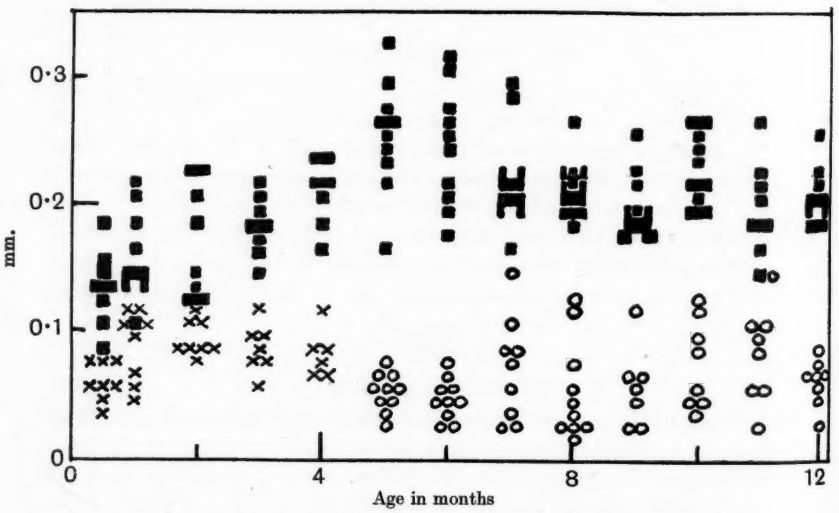

Fig. 2. Breadth of suprarenal cortex in female mice. Permanent cortex: squares; transitory cortex: crosses; perimedullary fibrous band: circles.

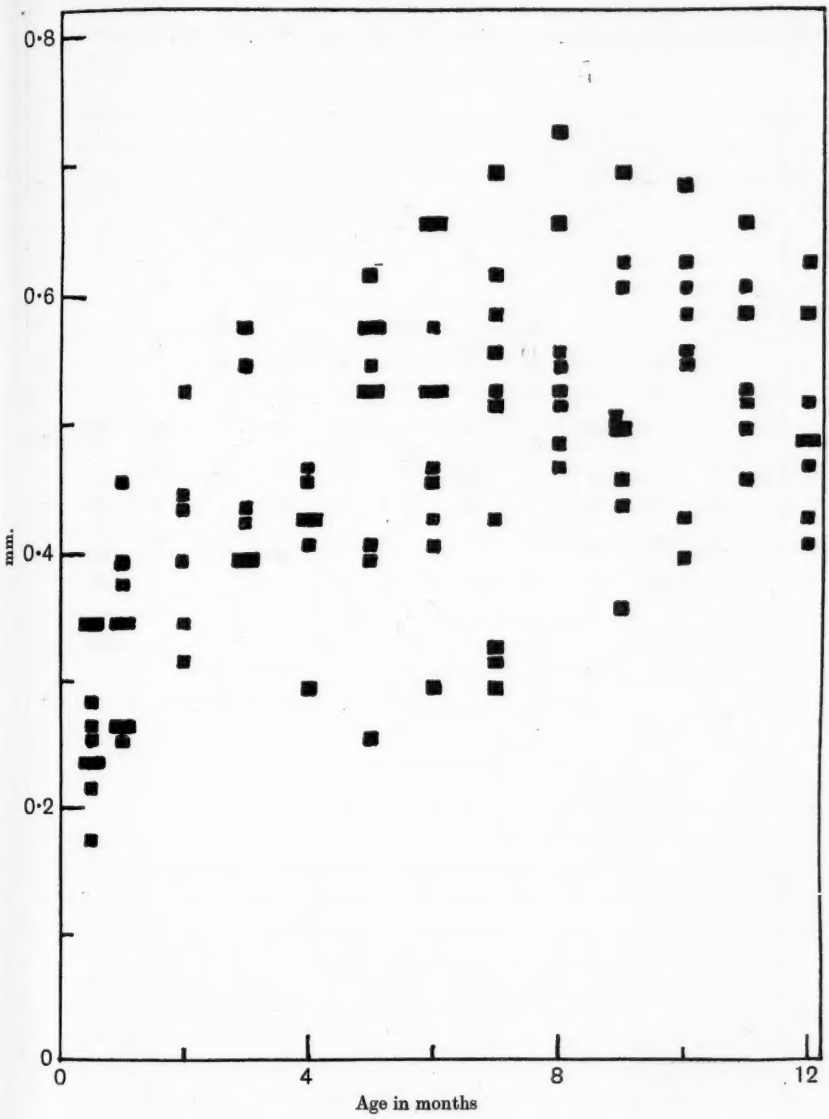

Fig. 3. Breadth of suprarenal medulla in male mice.

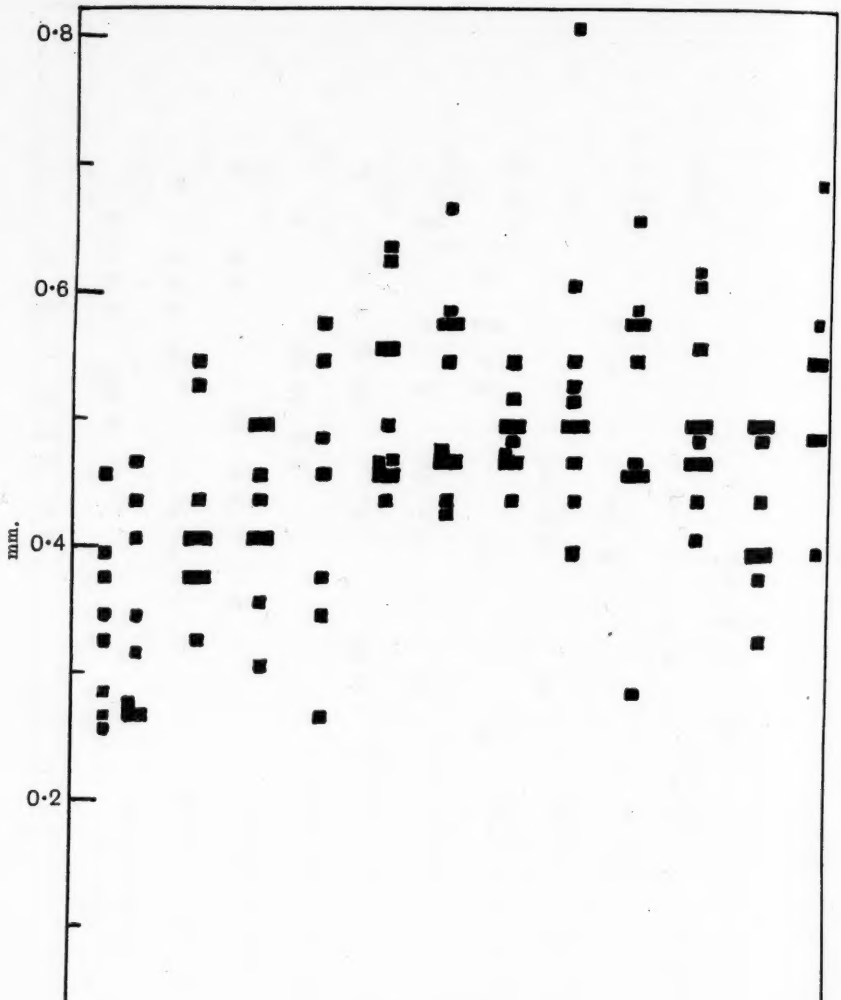

Fig. 4. Breadth of suprarenal medulla in female mice.

The lowest point of the middle of such a block marks the breadth. In figs. 1 and 2 the breadth of the transitory cortex (*X* zone) is indicated by crosses, that of the perimedullary fibrous band that succeeds the transitory cortex, by circles.

Breadth of permanent cortex

This is shown in fig. 1 for males and in fig. 2 for females. The average breadth of permanent cortex in both sexes is about 0·2 mm. This value is attained in males at 1 month, in females at 4 months. Before this epoch the female average is lower than the male average, but steadily rising. The breadth of permanent cortex varies widely within each age group. The range of variation is about the same at all ages and in both sexes.

Breadth of transitory cortex

The average breadth of transitory cortex is 0·03 mm. in males at 0·5 month (fig. 1, crosses). The variation is greatest at 1 month. The transitory cortex had disappeared from four of the eight glands measured at 1 month, hence the average is the same as at 0·5 month, viz. 0·03, although the range of variation is wider. In females the average breadth of transitory cortex attains 0·08 mm. at 1 month, remaining at this level until 4 months (fig. 2, crosses). The perimedullary fibrous band succeeding the transitory cortex is rarely of measurable breadth in males: in females, on the other hand, its average breadth is 0·06 mm. (fig. 2, circles).

Breadth of medulla

This is shown in fig. 3 for males and fig. 4 for females.

The average breadth of the medulla increases in both sexes until about 5 months. Thereafter it remains at about the same level in both sexes, viz. 0·5 mm. The range of variation in each age group is wide.

Discussion

Measurements

The minor axis, defined above, is the most suitable place for measurements of the mouse suprarenal, because the breadth of the cortex here varies least over unit distance. The cortex is rarely of the same breadth on both sides of the medulla, which as a rule appears to be placed eccentrically in the cortex. Sometimes a relatively thin shell of cortical tissue covers the medulla on one side of a longitudinal section. In this event the cortex on the other side is much broader. When the breadth of the cortex at both ends of the minor axis is averaged, the variations in a group of glands are much less than they would be if the cortex were measured at one end only of the minor axis in each gland. The phenomena noted are presented equally by permanent cortex, transitory cortex, and the perimedullary fibrous band that succeeds it.

The medulla is not always broadest at the minor axis. Its longest transverse diameter often occurs between the minor axis and the paravenous pole. It was desirable, however, to make all the measurements along one readily

identifiable line, the minor axis. Hence the measurements of the medulla plotted in figs. 3 and 4 do not always represent the longest transverse diameter of the medulla. It would be difficult to determine accurately the total amount of medullary tissue present in any gland, for as much as one-half of the area of a central section of the medulla may be occupied by blood sinuses when these are dilated.

The measurement of three sections eliminates the risk of gross errors, which are sometimes made if only one section is measured.

Growth of the suprarenal

In both sexes permanent cortex increases in breadth as long as the transitory cortex is present. When the transitory cortex has disappeared there is no sex difference in the breadth of the permanent cortex, hence in the female it increases in breadth more slowly than in the male. Since the transitory cortex persists longer in the female than in the male, permanent cortex is broader in the male than in the female until the epoch at which female transitory cortex has disappeared.

The growth of the medulla shows the same time relations in both sexes, being complete at about 5 months. This identity is interesting as suggesting that there is no relation between the growth of cortex and medulla. If such a relation existed, the medulla might have been expected to reach its adult breadth at the same time as the permanent cortex in both sexes.

When the transitory cortex has disappeared, the only sex difference is the presence in the female suprarenal of a broad perimedullary fibrous band.

Summary of part I

1. The permanent cortex of the mouse suprarenal increases in breadth in both sexes as long as the transitory cortex is present.

2. The average adult breadth of the permanent cortex in both sexes is 0·2 mm.

3. Since the transitory cortex lasts longer in the female than in the male, the permanent cortex increases in breadth more slowly in the female than in the male.

4. The medulla attains its adult breadth of 0·5 mm. at about 5 months in both sexes.

5. This identity of the growth phenomena of the medulla in both sexes suggests that the growth of the medulla is unrelated to the growth of the cortex.

6. When the transitory cortex has disappeared the presence in the female suprarenal of a broad perimedullary fibrous band is the only sex distinction.

PART II. MITOSIS

No systematic study of the natural frequency of mitoses in the suprarenals of the laboratory animals appears to have been made. The available literature, summarised by Jackson (1919), contains only casual observations.

The following study of the natural frequency and distribution of mitoses in the mouse suprarenal was made to furnish a basis for the interpretation of experimental findings and to determine the mode of growth of the transitory cortex.

Material and methods

The material described in Part I was used.

Mitosis counts were made of 107 glands from 57 males and of 115 glands from 61 females. Three sections of each gland were systematically swept for mitoses with a 1/12 oil immersion, and the situation and phase of each mitosis noted. Permanent cortex, transitory cortex and medulla thus yielded three values each. The highest of these was taken as the mitosis count.

Results

The mitosis counts for permanent and transitory cortex are shown in Tables I and II respectively.

Table I. *Natural frequency of mitoses in permanent cortex of mouse suprarenal*

Age (days)	Males	Average	Females	Average
15–17	16 28 22 26 .	19	18 9 29 – 13 .	16
	12 – 12 18 .		– 10 19 14 – .	
28	9 6 6 13 .	8	19 18 – 18 5 2	9
	6 5 2 17 .		6 6 4 – 6 3	
57	– 2 2 . .	2	17 26 29 0 . .	15
	0 1 4 . .		18 12 18 0 . .	
85–86	2 1 2 – 3	2	0 0 0 0 . .	0
	1 – – 2 –		0 0 0 0 . .	
111–112	2 1 0 . .	1	2 0 0 1 . .	1
	1 0 1 . .		1 0 1 0 . .	
141	0 0 0 1 0	0	1 – 0 1 1 .	1
	0 0 0 0 0		0 1 1 0 0 .	
167	0 0 1 0 1	1	0 0 1 1 1 .	0
	0 0 1 2 0		1 0 0 0 0 .	
201	2 0 1 2 0	1	0 0 0 0 1 .	0
	0 0 3 0 1		0 2 0 1 0 .	
227	1 0 1 0 .	1	0 0 0 0 – .	0
	0 0 2 0 .		0 0 0 0 0 .	
256	0 1 3 1 1	1	0 0 0 0 0 .	0*
	0 0 0 2 1		0 0 0 0 0 .	
280	3 0 0 0 0	1	0 0 1 1 0 .	0
	0 0 0 0 4		0 0 2 0 0 .	
310	0 2 10 0 –	2	0 0 0 3 . .	1
	0 2 1 0 0		0 1 0 4 . .	
336	5 1 0 2 .	3	3 0 1 0 . .	1†
	8 1 0 4 .		1 1 2 1 . .	

* 252 days. † 336–338 days.

Table II. *Natural frequency of mitoses in transitory cortex of mouse suprarenal*

Age (days)	Males	Average	Females	Average
15–17	19 12 13 9 20 – 11 17	14	4 8 5 – 7 . – 8 4 14 – .	7
28	0 – – 1 0 – – 2	1	4 20 – 3 1 0 4 7 1 – 0 0	4
57	. . . . 	.	4 2 1 1 . . 4 0 1 0 . .	2
85–86	. . . . 	.	0 0 0 0 . . 0 0 0 0 . .	0
111–112	. . . . 	.	0 0 0 0 . . 0 0 0 0 . .	0

Explanation of Tables I and II

Each entry represents one gland. For each age group of each sex there are two rows of figures. Those in the top row represent left glands, those in the bottom row the corresponding right glands. A cipher denotes a gland in which no mitoses were seen. A dash indicates an uncounted gland of a pair, or a gland from which transitory cortex had disappeared. The entries in Tables I and II correspond: e.g. in the left gland of the first male at 15–17 days permanent cortex contained 16 mitoses (Table I), transitory cortex 19 (Table II).

Mitoses in medulla

Mitoses in the medulla were rare. Two male glands at 15–17 days showed one each, one showed two. At 28 days, one gland showed one, one showed two. One gland at 111–112 days, one at 310, and three at 336, showed one each. One female gland at 15–17 days, three at 28, and one at 57, showed one each.

Frequency of different phases

The incidence of different phases of mitosis in the cortex is shown in Table III. The counts of all three sections of each gland, giving a total of 1660 mitotic figures, were used to determine this.

Table III. *Percentage incidence of different phases of mitosis in permanent (PC) and transitory (TC) cortex of mouse suprarenal*

Phase of mitosis	Males		Females		Average
	PC	*TC*	*PC*	*TC*	
Monospireme	59	52	51	42	51
Monaster	11	10	11	23	14
Diaster	3	3	2	5	3
Dispireme	27	35	36	30	32
Totals	100	100	100	100	100

Of the total eighteen mitoses seen in all sections of the medulla, nine were monospiremes, eight monasters, one a dispireme.

Distribution of mitoses

In the permanent cortex mitoses were commonest immediately beneath the capsule of the gland and rare elsewhere. They occurred throughout the transitory cortex. Comparison of counts from the same gland shows that the absolute number of mitoses in transitory cortex was usually less than that in the permanent cortex. The area of the part of permanent cortex where mitoses were frequent, however, exceeded that of the immature transitory cortex, and the actual frequency of mitotic figures in unit areas of both was about the same. Medullary mitoses were commonest at the periphery, but sometimes occurred elsewhere.

Absence of amitosis

No evidence of amitotic division was found. The resting nuclei of cortical cells appear circular or oval in section, and I have never seen irregular forms. The nuclei of the cortical stroma cells, however, though normally fusiform, vary much in size and shape. It is possible that some of these variants might be mistaken for nuclei of cortical parenchyma cells dividing amitotically.

Normal polar contouring

Hoerr (1931) observed that in guinea-pig suprarenals in which mitosis was active the cortical cells had convex inner borders and concave outer borders. This appearance, which he termed "polar contouring," is normally visible in the outer third of permanent cortex of the mouse suprarenal. It varies much in degree, but does not seem to depend on the number of mitoses present, since in the material here discussed it was less conspicuous in the immature glands than in adult glands showing few or no mitoses.

Discussion

Highest normal mitosis counts

Tables I and II show that after 2 months of age mitoses are rare in glands from both sexes. The highest count in permanent cortex in three sections of a gland exceeded four in only three instances among mice of both sexes aged 3–12 months, viz. in a male at 310 days (ten mitoses in one gland) and a male at 336 days (five and eight mitoses). The average values for the age groups giving the three high counts mentioned were two and three respectively.

Mitosis and growth

Table I shows that mitoses were numerous in both sexes while the permanent cortex was broadening. Mitoses were rare in males at 2 months, but still numerous in females. At 3 months they were rare in females. These results show that the immature permanent cortex increases in breadth by cell division at the periphery. Table II shows that mitoses were frequent in the male transitory cortex at 0·5 month and in the female transitory cortex up to 1 month. A few mitoses occurred in the female transitory cortex at 2 months: none were seen later.

Origin of transitory cortex

As shown above, in permanent cortex mitoses are rare except at the periphery, but occur throughout the transitory cortex. This demonstrates that transitory cortex increases in breadth by cell division and not by a change in the appearance of cells in the inner layers of permanent cortex. Whether transitory cortex cells are originally derived from permanent cortex cells is undetermined.

Frequency of spiremes

Table III shows that in permanent and transitory cortex of both sexes the phases of mitosis in order of decreasing frequency were monospiremes, dispiremes, monasters, and diasters. It is possible that some figures taken as monospiremes may have been members of dispiremes whose second members were not visible in the section, and also that some figures reckoned as dispiremes may really have been adjacent monospiremes, two adjacent cells chancing to be about to divide. The frequency of spiremes in the suprarenal was noted by Kolmer (1918) and Hoerr (1931) who attributed it to the long duration of the prophase. The fact could be more simply put by saying that the aster stages are more quickly traversed than the spireme stages.

SUMMARY OF PART II

1. Mitoses were numerous in both permanent and transitory cortex of the mouse suprarenal while these were actively growing.

2. Mitoses in permanent cortex were commonest in the subcapsular layers of cells, rare elsewhere.

3. Mitoses occurred throughout the transitory cortex.

4. Mitoses were rare in the medulla.

5. The phases of mitosis in permanent and transitory cortex of both sexes were in order of decreasing frequency, monospiremes, dispiremes, monasters and diasters.

6. In adults the highest average number of mitoses was three: counts up to ten were found in single glands.

7. Polar contouring is normal in permanent cortex and its degree does not seem to depend on the degree of mitotic activity.

8. Permanent cortex increases in breadth by cell division at the periphery.

9. Transitory cortex increases in breadth by cell division, not by modification of permanent cortex cells.

10. No evidence of amitosis was found.

I am indebted to Prof. S. L. Baker for his helpful criticism, and to Prof. J. S. B. Stopford for his interest in the work.

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THE CLASSIFICATION OF THE UPPER LIP IN MAMMALS

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The generally accepted description of the development of the upper lip, in the definition it makes of the relative contributions of the maxillary and fronto-nasal processes to the lip, does not adequately explain certain facts of considerable importance. I refer especially to the fact that it does not account for the different varieties of the upper lip found in the mammalian class, nor can there be explained in terms of it the profound change in the region of the anterior nares which occurred in the phylogeny of the Primates and has resulted in the disappearance of the rhinarium. I have found also that certain details of the malformations of the upper lip which occur in man are not readily explained if the current descriptions of development are accepted. I have made, therefore, as a preliminary to the study of its development, a survey of the different kinds of upper lip found in the mammals; and the results of this investigation indicate, I think, that the modification of the description of the development which I shall advance is necessary.

If the upper lip is used as the criterion for classification, the mammals can be best arranged, I believe, in five groups. These groups are distinguished by the relationships of the rhinarium to the portion of the lip originating from the maxillary processes[1]. It is generally considered that the rhinarium is derived from the fronto-nasal process and my embryological material appears to support this opinion[2].

The classification is applicable to all the mammals I have examined; certain highly specialised forms, however, which have not been available to me, may require an addition to the scheme I have suggested. I think that this is unlikely, for though in the elephant and tapir the development of a proboscis has modified the upper lip very considerably, the descriptions in the literature of the foetal conditions show that the different labial components can be distinguished; and, in those mammals which have a rostral-like projection of the upper jaw (the myrmecophagous species and many insectivores) the component parts of the upper lip are also well shown, sometimes with

[1] The classification is thus based on the characters of the lip itself and on its mode of development: it does not take into consideration the differences due to variations in the neighbouring structures, for example, the amount of protrusion of the jaws or the position of the narial apertures.

[2] I shall discuss this question in a later paper, but it may be noted here that even if the origin of the various parts of the lip were not as suggested in this paper, the classification given still rests on a valid description of the different kinds of lips.

diagrammatic clearness (fig. 2). The parts of the upper lip are, therefore, always at least fairly well defined even when modifications of the surrounding parts considerably alter its shape and position. This fact lends support to the conclusion that the relationship of the rhinarium (fronto-nasal process) to the lateral portions of the upper lip must be of considerable importance.

The term *rhinarium* has been used in recent literature in several different senses. It is taken in this paper to mean the area of modified skin which surrounds the nostrils and extends into the upper lip of many mammals. It is characterised by a very sensitive and usually coriaceous surface with many mucous glands, and the relative or complete absence of hairs. Wood Jones (1) has applied the term to the region of the anterior nares in the anthropoid apes and man. The condition of this region in the higher Primates, however, is so very different from that occurring in the lower types that the use of rhinarium as a descriptive term for the circum-narial region in them does not seem justifiable. This applies particularly to the use of the term in describing the condition found in man; for here the development of the nose and its vestibule has completely replaced the rhinarium of the lower mammals. It is much more satisfactory, as I consider will emerge in this paper, to reserve the term for the specialised area found in the lower mammals; the term should not be used in descriptions of the higher Primates unless qualified by such an adjective as "aborted." The loss of the moist glandular rhinarium is, in fact, as Pocock (2) and Wood Jones have shown, one of the considerable features that has accompanied the "recession of the snout" found in *Tarsius* and the Anthropoidea.

I have classified the mammals in groups (I to V) in the order which appears to explain the differences between them (fig. 1 A–E). The classification, while distinct, is not to be regarded as absolute, for some mammals show a combination of the characters of two of the groups; these types of lips, however, are of course still explicable on the same embryological basis which explains the conditions found more frequently.

Class I (fig. 1 A). The upper lip is formed by lateral hair-covered maxillary processes and a median naked area of variable width, the labial extension of the rhinarium, which separates them; and this labial extension of the rhinarium possesses a definite median groove which probably represents the line of fusion of the two median nasal processes (the globular processes of His), for the whole area is derived from the fronto-nasal process. Examples: *Dasyurus, Thalyacinus, Tamandua, Speothos, Chrysocyon* (Pocock), and most of the Lemuridae.

Class II (fig. 1 B). This is very similar in its main characters to Class I but the median groove of the rhinarium has become much less evident or is absent. It would seem that in this group the fusion of the globular processes is more complete than in Class I. These two classes are obviously much alike, and the important fact in each class is the presence of a naked median strip which extends from the circum-narial rhinarium above to the labial margin below and which is developed from the fronto-nasal process. This portion of the lip remains throughout life as an area showing the characters of the rhinarium

and greatly differing from the lateral portions of the lip which are developed from the maxillary process of each side. Examples: *Cyclopes*, *Bradypus*, *Choloepus*. Intermediate between Class I and Class II are those mammals (e.g. *Galeopithecus*) which show a slight or an interrupted median groove.

Class III (fig. 1 C). The maxillary processes in this group cover over the labial extension of the fronto-nasal process. The medial edges of the maxillary processes meet or almost meet in the middle line in front of the labial rhinarium, but do not fuse with each other. The cleft between the two processes can be opened out and the deeply situated rhinarial portion of the lip exposed: and, when this is done, the lateral (maxillary) portions of the lip can be seen to fuse and to be continuous with the lateral margin of the fronto-nasal (rhinarial)

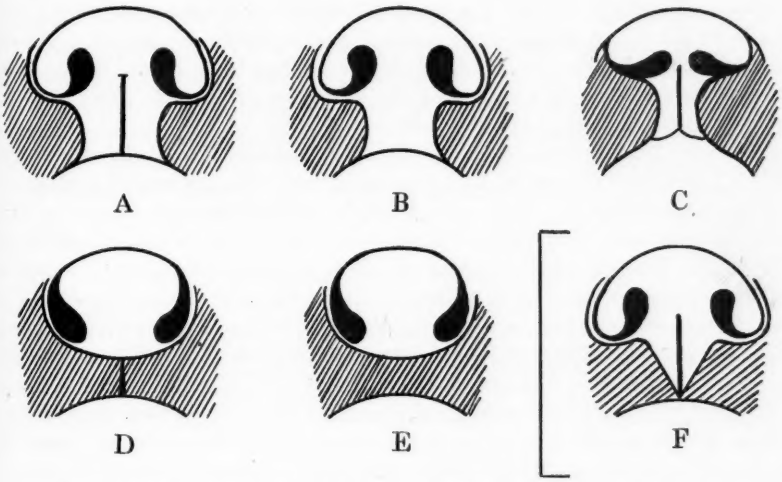

Fig. 1. Diagrams to show the different relationships of the rhinarium to the maxillary processes (shaded) in the mammals.

labial extension. This condition can be explained by postulating that this type of upper lip commences in a condition similar to the adult condition in the previous classes; at a subsequent stage the lateral (maxillary) portions of the lip grow more vigorously and eventually overlap the less rapidly growing portion derived from the fronto-nasal process. The study of a series of rabbit embryos shows that this is what actually occurs in the development of the lip in this species. The maxillary processes in the rabbit, having fused with the lateral edges of the fronto-nasal process, grow over in front of it, and at an early stage are united to one another by a great epithelial proliferation; the fusion persists for the greater part of gestation (see figs. 5–7). The exuberant growth of the entire substance of the maxillary processes causes these processes to extend oralwards lower than the labial extension of the fronto-nasal process

(see fig. 6); consequently the lower margin of the upper lip is formed only by the maxillary processes. At a later stage the epithelial fusion between the maxillary processes breaks down and a cleft is formed between them; this cleft must necessarily be through the entire lip below and be a surface cleft above. The labial extension of the fronto-nasal process in this class is not separated from the gum by a labio-gingival groove; probably this is because of its relative non-descent. Examples of Class III: Lagomorph rodents, Camelidae, Macropodidae.

Class IV (fig. 1 D). The maxillary processes meet and fuse in front of the labial portion of the fronto-nasal process and, though the fusion is permanent, a definite groove remains to show the line of fusion. This condition is a further stage of the condition found in Class III. The members of Class IV thus have the oral margin separated from the nasal rhinarium by a cutaneous hairy band indistinguishable from the surface of the rest of the face except that of the persistent nasal rhinarium. The surface of this band is broken by the median groove, which is always well marked. Examples of Class IV: *Orycteropus*, *Manis*, Canidae, Felidae, and Mustelidae.

A newly born puma in my possession shows a condition transitional between Class I and Class IV (see fig. 1 F). The upper part of the lip has a median area with all the characters of the rhinarium, including a median groove; on the oral margin, however, the lateral processes meet in the manner typical of Class IV. Most of the Lemuridae belong to the first two classes, having a definite labial extension of the rhinarium, but a Maholi Galago in my collection shows a completely hairy upper lip with a deep median groove (see fig. 3) and this lemur is therefore transitional between Class I and Class IV[1].

Class V (fig. 1 E). The maxillary processes in all the members of this class are fused in front of the fronto-nasal process without a groove being present to show the line of fusion. Certain members of this group have retained the nasal part of the rhinarium, which still forms a naked, coriaceous surface round the anterior nares (for example, *Sus*, *Equus*, and some of the small Carnivora). These constitute a first sub-class of this group. The whole of the rhinarium, nasal part and labial extension, in the other members of Class V, has been so radically modified that it is doubtful if the term should be retained in descriptions of these mammals. This second sub-class includes *Tarsius* (see fig. 4), the platyrrhine and catarrhine monkeys, the anthropoid apes, and man. It would seem that in this latter sub-class the process of maxillary overlapping has become so great that the nasal portion of the rhinarium has become covered over in a manner corresponding to the covering over of the labial portion.

The growth of the maxillary processes in the second group of Class V, which submerges the nasal as well as the labial portion of the rhinarium, is the end result of the progressive increase in their importance. The main factor causing the relative and absolute increase in the maxillary contributions to the face

[1] A similar description of this lemur has been given by Pocock.

would appear to be the decline in importance of the "oral sense" and the olfactory apparatus. This diminution in the importance of olfaction can be correlated with the decrease in the development of the fronto-nasal process, the maxillary processes becoming progressively more prominent in the formation of the definitive face. Another factor that may have had an influence on the process of substitution of maxillary processes for the fronto-nasal process is the marked increase in the mobility of the lips in the higher Primates. It is probable that the maxillary process of each side facilitates the migration of the hyoid musculature into the lips, since the labial extension of the rhinarium has little or no muscle and is usually bound down to the gum, no labio-gingival furrow being formed at this junction. This latter condition is shown in the hedgehog (fig. 2), where the rhinarium extends back to the palate so that the animal has a portion of its upper lip which never becomes a true labial flap. Other influences of possible importance in explaining the increase in the growth of the maxillary processes in the higher types have been considered; suckling in the higher types may be more dependent upon well-developed lips, and changes in dentition and methods of mastication may have caused a change in the functional requirements of the lips. These factors, however, appear to be of less importance as causes and more in the nature of possible results than the changes which accompanied the diminution in function of the olfactory and oral senses.

The classification of the mammalian upper lip given above implies an underlying similarity in the development of the lip in the different classes, the adult conditions being produced by changes in the relationships of the maxillary processes and the fronto-nasal process. The published descriptions of the development of the upper lip in the various mammals are very incomplete, especially in the rarer types which show peculiarities of particular importance. It is, therefore, impossible for me to give a complete account of the development of the lip in the five different classes in an attempt to illustrate the validity of the interpretation suggested. An examination of the embryos at my disposal, however, and especially the examination of a complete series of rabbit embryos, has not revealed any facts which make the scheme, or its interpretation, impossible to accept.

Frazer (3, 4) has described the development of the human upper lip in a manner slightly different from the generally accepted account. The scheme given in this paper to explain on an embryological basis the different types of upper lip found in the mammals is in entire accord with Frazer's descriptions of labial development. McMurrich, Keith, Bryce, Jordan, Prentiss and Arey, Broman, Corning, and the authors of other standard textbooks of embryology, on the other hand, describe the origin of the whole thickness of the median portion of the upper lip in man to be from the fronto-nasal process. The descriptions of His, the Hertwigs, and others of their time laid the basis for this interpretation and the current accounts (with the exception of Frazer's) are merely restatements of this older work.

The account given by Frazer of the early stages of facial development does not differ materially from the usual descriptions. He describes in the later stages, however, a growth of the maxillary processes over the lower end of the fronto-nasal process (i.e. over the median nasal process) so that the upper lip is formed superficially by the former structures alone. This growth medially of the maxillary processes is sub-epithelial in human development. The human embryos examined by me have shown me that this interpretation is correct; and in the rabbit I find that the course of development is comparable, but, though almost all of the overlap is of the entire process, in the middle line the overgrowth and the fusion are epithelial alone and the two processes do not fuse by their substance. This epithelial fusion breaks down at a later stage; and in the adult, if the maxillary processes are drawn aside, the fronto-nasal portion of the lip is seen in the floor of the cleft. The fronto-nasal portion of the upper lip is buried beneath the maxillary processes in a similar manner in man and is seen, in the later stages, only in cases of abnormal development.

The usual description of the production of unilateral cleft in the upper lip is that the fronto-nasal process does not unite with the maxillary process of the side on which the cleft is situated. It has been supposed that the cleft and a corresponding line on the other side of the lip are the lines of fusion of the maxillary processes with the fronto-nasal process, and that the tissue between the cleft and the corresponding line is of fronto-nasal origin. If this is so then a very grave difficulty is placed in the way of accepting the descriptions of the comparative formation and the development of the upper lip that have been suggested above. I think, however, that there is definite evidence to suggest an alternative explanation of unilateral labial clefts and one which does not conflict with the embryological interpretation that I have accepted. The medial margin of a unilateral labial cleft has muscle up to the edge of the cleft, a fact emphasised by Veau (5) and which I have confirmed in my specimens. A philtrum is present on the medial side of the cleft but this is always absent in cases of bilateral clefts of the upper lip. These facts suggest that a unilateral cleft is between the maxillary process of one side and, on the other side, the maxillary process (superficially) covering over the fronto-nasal process (deeply). The isolated lower end of the fronto-nasal process in a bilaterally cleft lip is small, it has no musculature, and is consequently very thin. It never shows a philtrum. The size and extent of the isolated process in bilateral cleft are due to two facts: (*a*) There is a tendency for the fronto-nasal process to attempt to fill the gap left by the failure of union. This compensation makes any attempt to determine, from the malformed condition, the part contributed by the median nasal process to the normal adult upper lip of very doubtful value. (*b*) The failure of the maxillary processes to fuse with and to overlap the fronto-nasal process in its lower part results in the columella of the nose not being properly formed. It is almost as if in normal development the maxillary processes could be regarded as "strapping back" the median nasal process and preventing it from growing

forward with the upper part of the fronto-nasal process which is forming part of the nose. The result is the production of the nasal columella. When the action of the maxillary processes is not present, that is in bilateral cleft of the upper lip, then the columella is very short. The lower end of the fronto-nasal process then projects forwards with the upper end, and the tissue destined in normal development to become part of the columella remains as part of the isolated median portion of the lip between the two clefts[1].

Certain types of labial abnormality show complete absence of fronto-nasal process in the upper lip, which is then formed entirely by the meeting of the two maxillary processes. This is the condition found in cases of cyclops with a proboscis; yet in these the maxillary upper lip often shows a well-developed philtrum and there is, of course, no possibility of a contribution from the fronto-nasal process. Median clefts of the upper lip result from failure of downgrowth of the fronto-nasal process, the maxillary processes not compensating for this failure. The failure of downgrowth may be complete; the resulting condition is arhinencephaly with median cleft lip, the cleft being between the two maxillary processes. The failure of downgrowth may be partial with development of an external nose, but the median process fuses only with the upper portion of the maxillary processes so that there is a deep median cleft of the upper lip.

Another fact of some corroborative value is found in the development of the labial frenulum. This is developed normally in a specimen of bilateral cleft lip at my disposal. The frenulum appears to be developed from the fronto-nasal process, that is, it represents the non-formation of the labio-gingival sulcus. The significance of this is evident when the marked development of the frenulum in the lemurs is remembered. The labial rhinarium in these Primates is well developed and the frenulum is large. The labial rhinarium of the higher Primates is aborted and the reduction in the development of the fronto-nasal process has been accompanied by a marked reduction in the size of the frenulum. Even in the isolated fronto-nasal process of abnormal development, however, the frenulum is present.

The philtrum in man is thus different from the philtrum which has been described in other mammals. The philtrum of the other types is simply the median groove found in Classes I and IV of my scheme, that is, it is either the median groove in the labial extension of the rhinarium, or the groove marking the meeting of the two maxillary processes in front of the fronto-nasal process. The philtrum in man is due to a heaping up of the maxillary mesoderm on either side of the middle line, but I have not enough material at present to give a complete account of its development. It is interesting, however, to find that a philtrum is not present in cases of bilaterally cleft lips (although it has been figured in several published sketches of the condition but never in photo-

[1] At the meeting of the Anatomical Society in June 1932 Frazer stated that in his opinion there is a maxillary contribution to the median process; that is that fusion having occurred between the elements of the lip a cleft is secondarily formed. A portion of the maxillary process might reach the isolated median process *via* the lower end of the nose.

graphs). When the upper lip is formed only by the maxillary processes, in cases of cyclops, a philtrum may be present.

I am indebted to Prof. Le Gros Clarke for the head of *Tarsius* which is figured, and to Prof. Walmsley who suggested the subject of this paper to me as one deserving attention and who helped me with much kindly criticism.

SUMMARY

1. Certain discrepancies in the current accounts of the development of the upper lip are referred to.

2. A classification of the mammalian upper lip is suggested which appears to allow of embryological interpretation of the different varieties of the upper lip.

3. The different varieties of upper lip appear to result from different relationships which exist between the fronto-nasal process (mesially) and the two maxillary processes (laterally).

4. An attempt is made to explain the teratology of the upper lip on the mode of development suggested by this study.

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EXPLANATION OF PLATE

Fig. 2. A photograph of the upper lip in the hedgehog seen from below. The rhinarium is markedly different from the surrounding area and its labial extension reaches back to the palate. There is a deep median groove in the labial portion of the rhinarium.

Fig. 3. A photograph of the rhinarium and upper lip in the Maholi Galago seen from below. The upper lip is seen to have a hair-covered surface up to the median groove, which is deep and wide. This species appears to be intermediate between the type of lip in which there is labial extension of the rhinarium and the type in which the maxillary processes meet and fuse in front of the fronto-nasal process.

Fig. 4. A photograph of the upper lip of *Tarsius* seen from below. This lip belongs to Class V of the scheme.

Fig. 5. Photograph of a horizontal section through the lip region of a 35 mm. rabbit embryo. The maxillary processes (*M.*, *M.*) are seen on either side and the fronto-nasal (*F.N.*) forms the deep bridge joining them. The epithelial proliferation, to which attention is drawn in the text, is seen both in front of and behind the fronto-nasal process.

Fig. 6. Photograph of a section at a lower (more oral) level of the embryo shown in fig. 5. At this level only the maxillary processes are shown; they are joined by the epithelial proliferation alone.

Fig. 7. Photograph of a transverse section through the upper lip of a 42 mm. rabbit embryo. The overlap of the fronto-nasal region by the maxillary processes is shown. The epithelial fusion between the processes is still present.

Fig. 2.

Fig. 3.

Fig. 4.

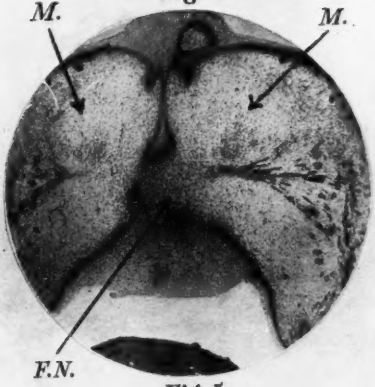

Fig. 5.

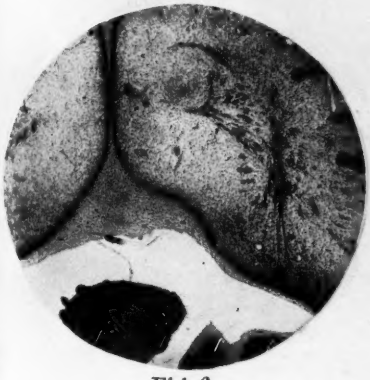

Fig. 6.

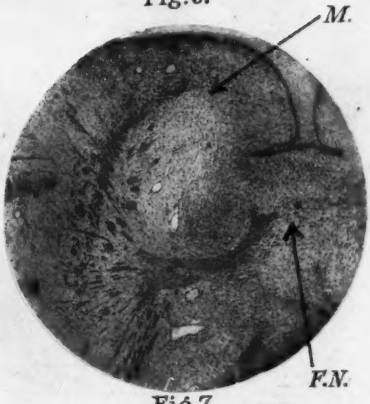

Fig. 7.

THE DISTRIBUTION OF VASO-CONSTRICTOR FIBRES IN THE LIMBS

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THE paper in the last number of this *Journal* by Woollard and Phillips (1) raises a number of interesting points, but it appears to us that some of the deductions from the experiments are apt to be misleading and some of the inferences are not fully warranted. At a time when the subject of the nervous control of blood vessels is arousing so much attention in the minds of clinicians and laboratory workers, it is particularly important to avoid any misunderstanding. It is in the hope of clearing up certain of the difficulties we encountered when reading this paper that we wish to discuss some of the matters raised in the light of our own observations and experience.

It is well known from clinical observations upon patients suffering from complete division of peripheral nerves that the sudomotor and pilomotor fibres are distributed to the same area of skin as the sensory fibres of the nerve. It is also evident that the vaso-constrictor fibres to the small superficial blood vessels have a distribution which is identical with that of the sensory fibres to the skin. It is often possible soon after one of the larger nerve trunks of the upper limb has been divided to define the extent of the cutaneous anaesthesia by the hyperaemia consequent upon the loss of vaso-constrictor fibres to the superficial vascular channels. Thus it seems to be reasonable to conclude that the blood vessels of an area of *skin* receive their vaso-constrictor supply from the nerves which provide the same cutaneous area with sensory fibres. From the study of patients suffering from division of the nerve roots or cords of the brachial plexus it also seems probable that the vaso-constrictor supply to the *superficial tissues* is arranged in a segmental manner. The experiments described by Woollard and Phillips do not appear to present very direct information upon this latter point, but they do confirm the clinical evidence regarding the distribution of vaso-constrictor fibres conducted by peripheral nerves to the skin.

It appears to us, however, extremely important to stress two facts regarding these observations and the deductions from the experiments described by Woollard and Phillips. In the first place it is necessary to emphasise the point that both the clinical and experimental evidence refers only to vaso-constrictor fibres. The profound vaso-dilatation, whatever its origin may be, succeeding irritative lesions of such nerves as the median or ulnar, is not confined to the cutaneous territory of the affected nerve. Studies of cases of

thermalgia(2) show that the extent of the cutaneous hyperaemia and hyperthermia commonly exceeds the normal sensory distribution to skin. Secondly, it is of fundamental importance to direct attention to the fact that our clinical and their experimental observations only supply information regarding the distribution of vaso-constrictor fibres to the vessels supplying superficial tissues. The experiments do not appear to provide any direct evidence about the distribution of vaso-constrictor fibres to the deeper vessels: in fact, from our experience, the records suggest that the dilatation of the larger blood vessels in the palm (and possibly the digital arteries) must have been slight in consequence of the injections into the ulnar and median nerves described by Woollard and Phillips. It is reported that after injection of the ulnar nerve at the elbow the surface temperature of the little finger was raised only 2° C. (1·3° C. on the dorsum), and along the ulnar border of the hand the rise was about 1° C. Following injection of the median nerve at the wrist, a rise of 2° C. is recorded, whilst after injection of the same nerve at the elbow the elevation of skin temperature of the digits ranged between 4·8° C. on the ring finger and 2·4° C. on the thumb. After suspension of the function of the vaso-constrictor supply to both the superficial and deep vessels of a part we find in healthy subjects a rise of about 8° C., sometimes as much as 10° C.(3). We submit, therefore, that the injections made by Woollard and Phillips have affected the deep vessels very incompletely, and that the experiments cannot be used to give precise information as to the source, extent or arrangement of the distribution of vaso-constrictor fibres in the median or ulnar nerve to the deeper vessels. In support of this contention, it is very enlightening to turn to the results of the injection made by Woollard and Phillips of the posterior tibial nerve close to the point where it divides into the medial and lateral plantars. In such an experiment the vaso-constrictors to both the superficial and deep vessels of the sole of the foot would be cut off and, in consequence, they record increases in surface temperature on the digits ranging from 7·4° to 8·1° C., which are consistent with our own findings. The injections of the median and ulnar nerves, in the light of the results of injection of the posterior tibial nerve and our own observations, seem to indicate that the distribution of vaso-constrictors to the deeper vessels in the palm is rather complex. There appears to be no evidence to justify any conclusion that the distribution of vaso-constrictor fibres to the deeper vessels follows such a simple arrangement as that observed in connection with the superficial vessels. To prevent misunderstanding later, we therefore insist that the conclusions regarding the limitation of vaso-constrictor fibres to the same territory as that innervated by the cutaneous sensory branches of a nerve, must be applied strictly to the superficial vessels supplying the skin. Although, in the sentence of their paper which precedes the summary, Woollard and Phillips state that it has not been possible, so far as they know, to determine what segmental nerve or nerves are reaching the large arteries (such as the brachial, radial or ulnar), it is not clear from the rest of the paper that their conclusions are confined to the vaso-constrictor fibres of cutaneous

vessels. We desire to draw attention to the fact that their experiments throw light only upon the superficial vessels going to skin. We think there is some indication from their experiments that the arrangement of the vaso-constrictor fibres to the vessels in the palm and their main branches is complex, and that there is considerable overlap in the distribution of branches from the different nerves. This is in accord with the results of an enquiry into deep sensibility (4) in which the arrangement of the sensory fibres innervating subcutaneous tissues was found to be both complex and variable. The small amount of information which is at present available, with reference to the distribution of vaso-constrictor fibres to the deep vessels of the palm, fails to suggest that these channels are supplied in a segmental manner.

In the early part of their paper Woollard and Phillips infer that, in a recent paper, we have suggested that the index finger comes within the territory of the first dorsal segment. Reference to our paper (5) will show that we state two facts based upon actual observations. First, that a bundle of sympathetic fibres in the lower trunk of the brachial plexus is pressed upon by a cervical rib: and secondly, that our cases (now six in all) show the greatest damage in the index finger. We drew from this no deduction whatever as to the distribution of the vaso-constrictor fibres, and the interpretation presented by Woollard and Phillips is unwarranted and mistaken. If a condition of spasm with thrombosis is produced in the larger vessels of a limb, then a particular digit may show a tendency to earlier gangrene than the others. This may depend on anatomical peculiarity or on predominant use of the digit. It does not necessarily have any relation at all to its vaso-constrictor supply.

In a later paragraph, Woollard and Phillips make reference to evidence brought forward by one of us (6) as to the innervation of the interphalangeal joints. After mentioning that they did not test particularly for heat and cold, the writers go on to state that "even with *complete digital anaesthesia* there was no loss of the sense of awareness of the position of the finger." The authors remark that they were surprised at this in view of the evidence brought forward by Stopford. We must admit that we are amazed at the presence of any form of sensation in a finger exhibiting complete digital anaesthesia. Obviously there is some mistake, either the method of investigation or the form of description demands correction. Work such as this of Woollard and Phillips is clearly of no value when employed in the criticism of observations (6) based upon a full sensory examination of fifty-one patients, in which definite peripheral nerves were known to be completely divided.

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A NOTE ON THE AFFERENT NERVE-SUPPLY OF THE FACIAL MUSCLES

By CECIL P. G. WAKELEY, D.Sc., F.R.C.S.
AND
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The interesting problem of the afferent nerve-supply of the facial muscles has hitherto been investigated by clinical and histological methods.

The cutaneous branches of the N. trigeminus are disposed superficially to the facial muscles and have thereby made clinical investigation a matter of some difficulty. Various opinions have been advanced—some observers coming to the conclusion that the VIIth nerve, after emergence at the stylomastoid foramen, is a purely motor nerve, others that it also contains afferent fibres.

Weigner (1905) examined the VIIth nerve in man histologically and stated that, at the stylomastoid foramen, it contains fibres of facial origin (i.e. motor fibres) and also fibres derived from the N. intermedius.

The problem does not appear to have been investigated experimentally. We came to the conclusion, however, that if the VIIth nerve were divided between the medulla and the internal auditory meatus, i.e. proximally to the geniculate ganglion, and time allowed for degeneration of the motor fibres, examination of the nerve would show whether medullated afferent nerve-fibres were present or not.

It was first found, in *Macacus Rhesus*, that, although the number of medullated nerve-fibres varies in various individuals, yet that in any one the number is equal on the two sides. Thus in one specimen 4096 medullated nerve-fibres were found in the right VIIth nerve just below the stylomastoid foramen and 4095 on the left.

In a second animal, under chloroform and ether anaesthesia, the VIIth and VIIIth nerves were divided internal to the internal auditory meatus. The head of the animal was held in a support, very similar to that which was used by the late Sir Victor Horsley. The skin over the occipital bone and neck was shaved and thoroughly cleaned with spirit. A curved incision was made from the mastoid process to the external occipital protuberance, and then downwards towards the spinous process of the second cervical vertebra. Haemorrhage from the scalp was controlled with pressure forceps. The muscles attached to the external surface of the occipital bone were stripped from their origin by means of a periosteal elevator; the bleeding from the muscles was not great but numerous emissary veins passing through the occipital bone caused a certain amount of trouble. Bone wax as devised by Horsley was the only method which controlled this bleeding; the wax being forced into the foramina with the

thumb. A small trephine hole was made over the left cerebellar fossa and a disc of bone removed. The opening was enlarged as far upwards and laterally as the lateral sinus, and downwards as far as the margin of the foramen magnum. The opening was limited medially by the attachment of the falx cerebelli. The dura mater was incised in a crucial manner and the left cerebellar hemisphere exposed. By means of a thin illuminated retractor the cerebellar hemisphere was slowly displaced inwards and a view of the internal auditory meatus was obtained. The VIIth and VIIIth nerves could be seen passing into the opening. A small blunt hook was passed round the nerves and a tenotomy knife was used to divide them. There was some haemorrhage from the division of the auditory artery and a little fall of blood pressure which, however, soon regained its former level. The dura mater was replaced over the cerebellum but was not stitched. The nuchal muscles were stitched with catgut and the skin with silkworm gut. The wound was painted with Whitehead's varnish but no dressings whatever were applied. As the animal was recovering from the anaesthetic it was noticed that facial paralysis was complete. The wound healed by first intention. The animal was very ataxic at first and during the first week after operation could not walk. The left eye was washed out daily with boric acid as the animal was inclined to fall and scratch the cornea. However, in three weeks the ataxia had almost disappeared and the animal was quite itself again and did its usual tricks on the trapeze. A month later an overdose of chloroform was given and the nerves dissected out. The right (intact) VIIth nerve, just below the stylomastoid foramen, was found to contain 4782 medullated nerve-fibres and the left (divided) nerve 359 fibres = 7 per cent. of those on the right. These persisting muscle-afferent medullated nerve-fibres, with their cells of origin in the geniculate ganglion were—like those on the right side—of all sizes from 2 to 12 μ in diameter and uniformly scattered in the nerve-trunk. Their receptors in the muscles have yet to be determined.

The facial muscles, then, like the masticatory muscles, have afferent medullated nerve-fibres passing to them, although the percentage is far less. It was shown by one of us, some years ago, that after division of both roots of the N. trigeminus proximally to the Gasserian ganglion, 34 to 36 per cent. of the medullated nerve-fibres persisted in the branches passing to the masticatory muscles.

Further investigations on the subject are in progress in the Hambledon Department of Anatomy of King's College. It would also be of interest to ascertain whether stimulation of the central end of the divided VIIth nerve produces any reflex effects, and this we propose to investigate.

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A REPORT ON THE SPINOUS PROCESSES OF THE CERVICAL VERTEBRAE IN A SERIES OF EGYPTIAN SKELETONS

By L. R. SHORE

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I. INTRODUCTION

In the *Journal of Anatomy* (vol. LXV, pt. 4) of July 1931, I published a report on the spinous processes of the cervical vertebrae of the native races of South Africa. This report contains a study, morphological and statistical in the main, of the forms of cervical spinous processes found in 71 Bantu and 12 Bushman skeletons, and a comparison of these with the cervical spinous processes of 11 European skeletons.

It does not appear that observations on the form of the cervical spinous processes of Man have often been made on a series as long even as 71 skeletons, though many authors have published notes on short series belonging to various races of Man.

The contributors to most textbooks in English make some such statement as that found in Morris' textbook (1): "...As a rule among Europeans, the second, third, fourth, and fifth vertebrae possess bifid spines...sometimes the sixth has a bifid spine, and, more rarely, the seventh presents the same condition....In the lower races of Man the cervical spines are relatively shorter and more stunted than in Europeans and, as a rule, are simple. The only cervical vertebra which presents a bifid spine in all races is the axis; even this may be non-bifid in the Negro, and occasionally in the European."

It was remarked in the report referred to above that "bifid" spine, or spinous process, is an ambiguous term and objectionable because the latinised form "spina bifida" conveys an entirely different meaning. In addition, the term lacks precision because two different types of cervical spines, or spinous processes, fall within the description of "bifid." On the one hand, "bifid"

spines may correspond, in a measure, to the forms shown in British text-books, with dorsal terminations deeply split, and with segments boldly divergent. On the other hand, certain "bifid" spines possess non-divergent segments. I suggested the name "bifurcate" for the first and "cleft" for the second. The cleft type I thought to be regressive.

Non-bifid cervical spinous processes constitute a majority in the skeletons of South African native races and show variations of form in different columns and even within a single column. In European skeletons also, non-bifid cervical spinous processes are found to form a proportion of the total which is not inconsiderable.

To return to the bifurcate forms: these spinous processes are peculiarly characteristic of European cervical columns. But it was shown in addition that differences of form occur in bifurcate cervical spinous processes; and there is reason to think that two forms or sub-types of bifurcate cervical spinous processes may bear racial significance.

The European material available for my other report contained skeletons of individuals from Northern Europe and from Sardinia in about equal proportions. Quite definitely it seemed that the cervical columns from Sardinia could be distinguished from the others by details in the characters of their spinous processes though bifurcate. In these cervical columns the average spinous process is less robust and less conspicuously bisected; the lateral alae are shorter and the angle of their divergence is smaller. In contrast: cervical spinous processes of robust build, broad-based and with alae both long and widely divergent—the unequivocal "bifurcate" type—seem to belong to columns derived from Northern Europe. The number of columns of each of these groups was small, Northern European 5, Sardinian 6; but these characters were consistent, and tentatively, pending correction or an opportunity of wider investigation, I called the two types of bifurcate cervical spinous processes "Mediterranean" and "Nordic."

Perhaps I used these names with too little justification; for the assumption that Sardinia furnishes a "fair sample" of the Mediterranean littoral underlies the use of the name. If I might anticipate the findings of the present survey, I would suggest that the presence in the bifurcate cervical spinous processes of skeletons from the Eastern Mediterranean also, *i.e.* from Egypt, of characters which closely resemble those described above does lend some support to my assumption.

The point of peculiar interest in the Bantu peoples is that their bifurcate cervical spinous processes, which account for 12 per cent. compared with 51 per cent. in Europeans, resemble those found in the Sardinian skeletons rather than in those of Northern Europeans in the proportion of roughly 4 to 1. There may be alternative explanations for this occurrence. This finding may be evidence of actual admixture between Arabs or other Mediterranean peoples and Bantus, possibly on the East Coast of Africa. Or the presence of cervical spinous processes of a form less conspicuously bifurcate may indicate an early

stage of a retrograde change in the Bantu column, perhaps antecedent to the form I have called "cleft."

It was this difference that seemed to be indicated, between the cervical spinous processes of Northern Europe and the Mediterranean, that prompted me to embrace with interest an opportunity to study the forms of the same structures in the skeletons of ancient Egypt at Cambridge.

Ancient Egypt probably contained a medley of races in its population in virtue of her former position as the centre of the Eastern World. The indigenous people of Egypt probably resembled other races of the Mediterranean littoral, and possibly absorbed as mercenaries, traders or slaves, strangers who may belong to the root-stock who peopled Northern Europe, perhaps from Asia Minor, or who possibly were true Northern people. On the other hand, a strain of Negroid peoples from Upper Egypt or from the Soudan, possible forerunners of the Bantu stock, may also have been assimilated.

The following pages contain an account of the morphological features of the cervical spinous processes found in a collection of skeletons of ancient Egypt, compared with the like structures found in skeletons of Northern Europe and of the Bantu races of South Africa.

II. MATERIAL

The material available for the study of Egyptian cervical columns is derived from the vertebral columns that correspond with the "Petrie" collection of skulls in the Anatomy School at Cambridge. This collection was excavated by Sir Flinders Petrie at Hierakonpolis and presented to the Anatomy Museum; it is stated to include the remains of the prehistoric and of the early dynastic races of Egypt. I have to acknowledge the kindness of Prof. Elliot-Smith, who writes me as follows: "While most of the skeletons are predynastic, i.e. earlier than 3400 B.C., they are mixed with others of the first three dynasties—say, until 3000 B.C. You can safely say that they are earlier than 3000 B.C."

Most of the columns are fragmentary, with very fragile and damaged bones. Unfortunately, the wear and tear of time and the disintegrating influences of excavation and of transport have fallen most hardly on the cervical vertebrae, and especially on the spinous processes.

I have preferred to make use of such cervical columns as are complete in order to give the reader an impression of the morphological characters of the spinous processes, though the number is no greater than 44. I have supplemented this 44 by the addition of 2 columns whose seventh unit is missing, and of 12 whose axis is missing; these include 3 from which both axis and seventh unit are missing. The total is now 58 columns, complete as regards the middle members.

The collection contains more than thrice as many columns in a more fragmentary state. No doubt it would have been possible, even from fragmentary columns, to assign vertebrae to their proper stations without considerable anatomical error. It would then have been possible to make a statement

of the character of the spinous process of each of the several vertebrae, based on larger numbers of each; but I have preferred to use smaller numbers of complete columns, because the presence or the absence of homogeneity of type of the cervical spinous processes within the individual column would in that case have been less apparent or, at least, a point not to be insisted upon.

The European material in the Anatomy Museum at Cambridge has been used for comparison and is presumed to be of Northern European origin. There are 11 fairly complete cervical columns recovered from excavations in East Anglia. These include 7 incomplete Saxon columns, placed at my disposal by Dr Duckworth for the purposes of this report. These last were excavated from the Bran Ditch at Melbourn in Cambridgeshire, the reputed site of a massacre of Saxons in the seventh century. A further 17 vertebral columns are unclassified, being mounted or strung together for anatomical demonstration. Some of these are not quite mature but all are considered to be of Northern European origin. A total of 28 European cervical columns has thus been secured.

The characters of the cervical spinous processes found in Bantu skeletons have been used for comparison with those of the other two races. The report published in this *Journal* is at hand and represents the results of a survey similar to that attempted in this place, on a material that is comparable in size. Suitability of this comparison in other respects will become apparent in the following pages.

III. THE OCCURRENCE OF BIFID AND OF NON-BIFID CERVICAL SPINOUS PROCESSES IN EUROPEAN, EGYPTIAN AND BANTU SKELETONS

In this section the terms "bifid" and "non-bifid" will be used as in the common terminology of anatomy without more precise qualification.

The skeletal material summarised above has been surveyed in order to determine the proportions in which cervical spinous processes are bifid and non-bifid in European and Egyptian skeletons.

The results of this survey are set out in graphic form in fig. 1. The *abscissae* represent the cervical vertebrae of each of the three races under comparison, set out from left to right in descending order. *Ordinates*, in the form of rectangles, have been constructed, each of a height proportional to the number of specimens of the several vertebrae which have been examined. The larger rectangles have been subdivided into black and white areas, which represent graphically the numbers of each vertebra which possess respectively bifid and non-bifid spinous processes.

The character of each spinous process has been classified as bifid or non-bifid according to its appearance in norma verticalis. The sharp narrow grooves, seldom exceeding 1 mm. in depth, that frequently mark the summits of the spinous processes in any region of the column, have been disregarded. These

shallow grooves are considered to be reminiscent of a bipartite stage in development, but not to be of further significance. The bifid character has been attributed only to those spinous processes in which the dorsal division is deep and decisive in its effect on the contour of the whole structure.

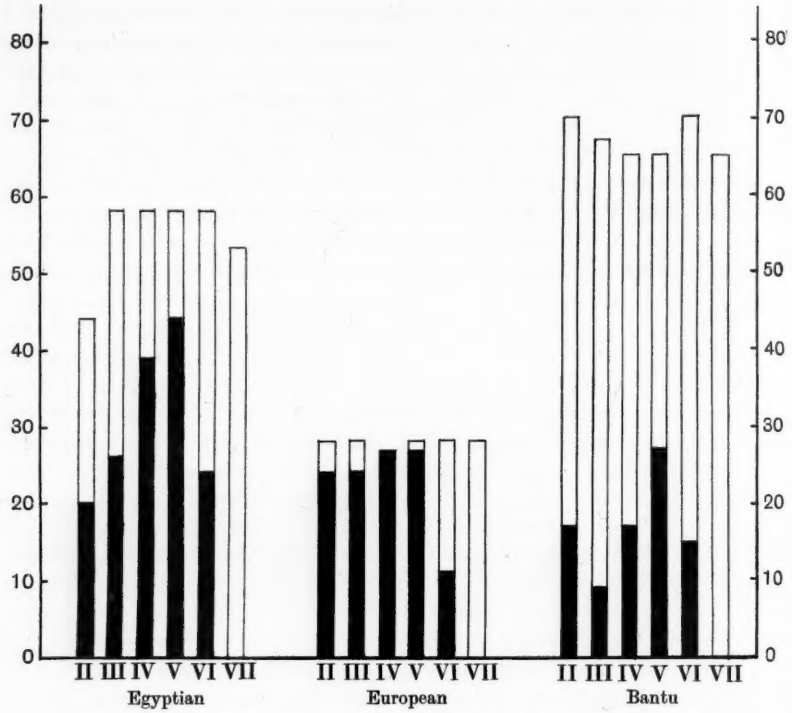

Fig. 1. This figure presents in graphic form the numbers of bifid and of non-bifid cervical spinous processes found in 58 Egyptian, 28 European and 71 Bantu skeletons. The abscissae represent the several vertebrae of the cervical column, set out for each of the three races in descending order from left to right. The ordinates represent the numbers of each vertebra examined. Rectangles in black represent numbers of vertebrae whose cervical spinous processes are bifid, and the white rectangles the numbers whose spinous processes are non-bifid. (From the data set out in Table I.)

The data set out in Table I, which form the basis of fig. 1, do not take account of divergence or of non-divergence of the segments of a bifid cervical spinous process. Attention will be given to this point in a later page.

Examination of fig. 1 will show the reader that the bifid character of the spinous processes is most marked in the European, least marked in the Bantu and intermediate in the Egyptian cervical columns. Indeed, the value for the Egyptian expressed as a percentage is very near the mean of the other two.

It is of some interest to note that the spinous process is most constantly bifid in the fifth cervical vertebra of Egyptian and Bantu columns, but in the fourth cervical vertebra in European columns. Some affinity between the Egyptian and the Bantu might be inferred from this fact alone. Cunningham (2) regards the third or the fourth cervical spinous process as the most constantly bifid, but Von Eggeling (3) the fifth.

Table I. *Bifid and non-bifid cervical spinous processes in European, Egyptian and Bantu skeletons*

		Vertebrae							
		II	III	IV	V	VI	VII	Totals	%
European	Bifid	24	24	27	27	11	0	113	67·66
	Non-bifid	4	4	0	1	17	28	54	32·33
	Totals	28	28	27	28	28	28	167	
Egyptian	Bifid	20	26	39	44	24	0	153	46·5
	Non-bifid	24	32	19	14	34	53	176	53·5
	Totals	44	58	58	58	58	53	329	
Bantu	Bifid	17	9	17	27	15	0	85	21·2
	Non-bifid	53	58	48	38	55	65	317	78·8
	Totals	70	67	65	65	70	65	402	

IV. GENERAL CHARACTERS OF THE CERVICAL SPINOUS PROCESSES FOUND IN EGYPTIAN COLUMNS

Fig. 2 contains representations of the several vertebrae, from the second to the seventh inclusive, of five Egyptian cervical columns viewed in norma verticalis. The vertebrae were carefully set in norma verticalis and outline tracings were made with the aid of the dioptograph, of natural size. Scales in centimetres accompany the tracings, so any reduction necessary for purposes of reproduction will affect tracings and scale in like proportion. Even a brief examination of the tracings in fig. 2 will impress the reader with the heteromorphous character of the spinous processes of these Egyptian cervical columns.

In writing my report on the spinous processes of the cervical vertebrae in the native races of South Africa, it seemed necessary to suggest names and a classification for the various forms exhibited by those structures in South African native skeletons. The number of different forms demanded a greater precision and consequent expansion of nomenclature. The same need is found in describing cervical spinous processes in Egyptian skeletons, but, fortunately, there is no need to alter or to expand nomenclature further. The names and the classification used previously seem serviceable, and some advantage is gained by having both reports in harmony.

Throughout this report the names used have been suggested by the appearances presented by the cervical spinous processes when viewed in norma verticalis.

The full classification follows; and descriptions of the various types will follow the classification seriatim.

A. Bifid: (1) Bifurcate.
(2) Cleft.

B. Non-bifid: (1) Acute.
(2) Obtuse.
(3) Pediculate.
(4) Clavate.

A. *Bifid cervical spinous processes*

It has already been remarked that the term "bifid" is unsatisfactory. In precise terminology the word means no more than "bipartite" or "bisected"; but when rendered into Latin, "spina bifida" conveys a meaning which is entirely fallacious in the present context. The segments of a bifid spinous process may diverge or may retain their parallelism. For the first, the name "bifurcate" is suggested, and for the second "cleft."

(1) *The bifurcate type* is illustrated in fig. 2 by the column on the right, No. 151, in its fifth and sixth members, and by many examples in fig. 3.

(2) *The cleft type* is shown in fig. 2 in the fourth and fifth members of column No. 193, and also in fig. 3 in the fifth member of the right-hand column.

B. *Non-bifid cervical spinous processes*

(1) *Acute*. This type is represented by flat-sided spinous processes which taper to a point in the mid-dorsal line. Specimens may be slender and long; they may exceed a centimetre in length in Bantu skeletons, but generally have been found smaller in the Egyptian. In the Egyptian skeletons they are very sparsely represented, and the description of the type is included for little better reason than to bring this report into harmony with the other. An example is shown in fig. 2 in the fourth member of column No. 151 on the right. Whole columns of this type are found in South African native skeletons and peculiarly in those of the Bushman.

(2) *Obtuse*. This type contrasts with the last. The name applies to the blunt-ended, irregular prominences which show little or no differentiation for

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Legend to fig. 2

Fig. 2. In this figure are set out tracings of the several vertebrae of five Egyptian cervical columns viewed in norma verticalis. The purpose is to show the different types of the spinous processes and the heteromorphous content of the cervical columns. No. 203, on the left, shows the pediculate type in the third to fifth units; No. 193 shows the cleft type in its fourth and fifth members, and the obtuse type in its axis; No. 209 shows the obtuse type in its third and fourth units; Nos. 99 and 151 have feebly bifurcated types in the fifth member of the first and in three of the second. The acute type is represented by the fourth unit of No. 151, and the clavate type by the seventh unit of each of the five columns. A centimetre scale is set on each side of the drawings.

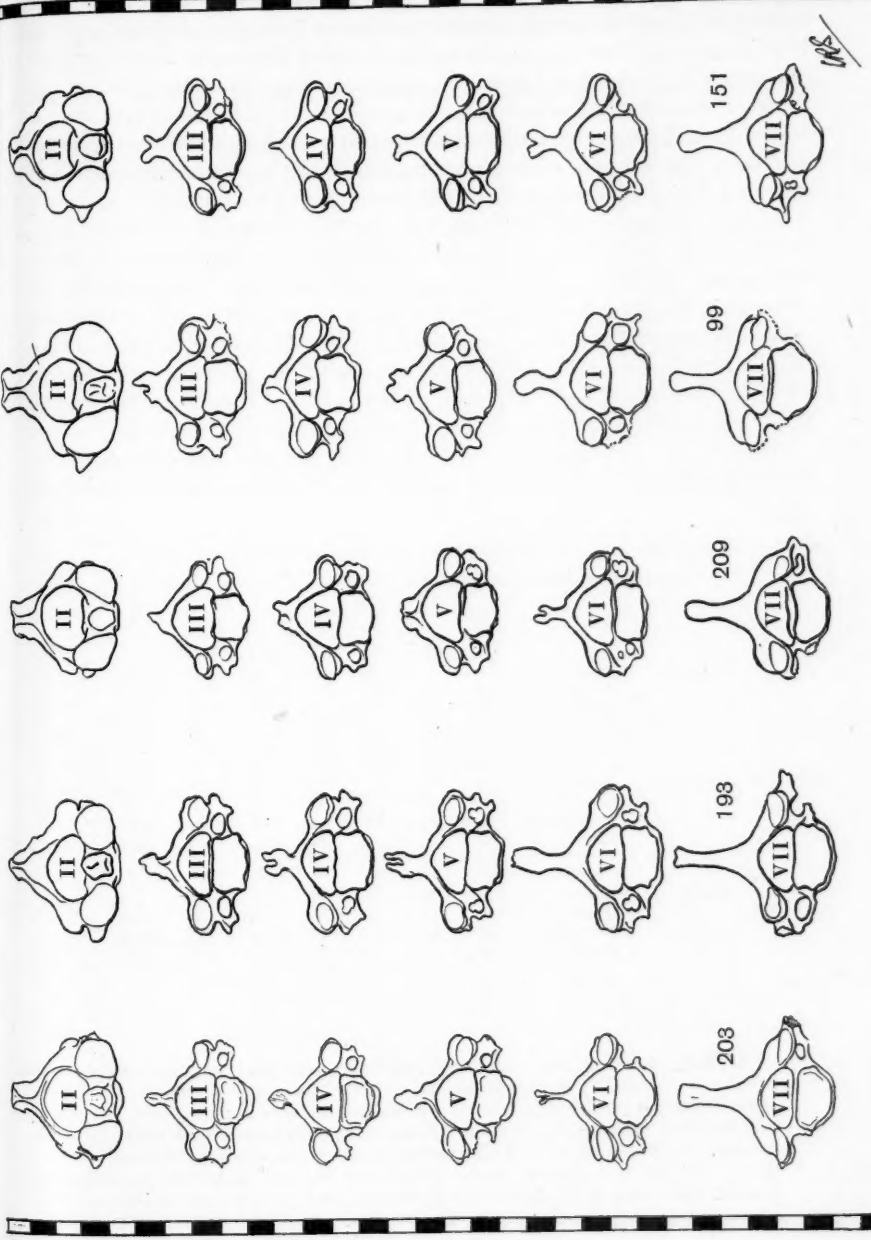

Fig. 2. (Scales in centimetres)

the attachment of muscle or of ligament. Specimens may be pyramidal or conical in shape, but seldom attain a centimetre in length. Fig. 2 shows the type in the axis of column No. 193 and in the third and fourth units of column No. 209. This type is less common in Egyptians than in Bantus.

(3) *Pediculate.* This name applies to a type of cervical spinous process that is stud-like. A blunt expanded end is attached by a short pedicle to the vertebral arch. The length of such spinous processes may be over a centimetre, but averages distinctly less than that of the type next to be described.

Column No. 203 on the left of fig. 2 shows three specimens of this type in its middle units. Such a cervical column would excite no curiosity in South Africa and would, *caeteris paribus*, be accepted as Bantu. The pediculate type is common in Egyptian skeletons also, and in this respect an affinity to the Bantu may be indicated, but uniformity of this type has seldom been shown by all the middle members of an Egyptian cervical column. In Bantu columns 20 out of 71 had cervical spinous processes of homogeneous type in all the middle members, and the pediculate type was represented by 13 of these 20.

(4) *Clavate.* A spinous process of this type is long and club-shaped, having an elongated stalk tapering to the middle both from the point of attachment

Table II. *The non-bifid cervical spinous processes in European, Egyptian and Bantu skeletons.* (*The axis is not included*)

		Vertebrae						
		III	IV	V	VI	VII	Totals	%
European	Acute	0	0	0	0	0	0	0·0
	Obtuse	1	0	0	0	0	1	2·0
	Pediculate	3	0	1	2	0	6	12·0
	Clavate	0	0	0	15	28	43	86·0
	Totals	4	0	1	17	28	50	
Egyptian	Acute	1	1	1	0	0	3	1·98
	Obtuse	5	0	1	0	0	6	3·97
	Pediculate	26	18	11	5	0	60	39·73
	Clavate	0	0	1	29	53	83	54·96
	Totals	32	19	14	34	53	152	
Bantu	Acute	6	8	7	0	0	21	7·87
	Obtuse	11	10	5	0	0	26	9·84
	Pediculate	41	30	24	19	1	115	43·56
	Clavate	0	0	2	36	64	102	38·63
	Totals	58	48	38	55	65	264	

Legend to fig. 3

Fig. 3. This figure presents tracings of the several vertebrae of five cervical columns. The column on the left possesses spinous processes of the familiar Northern European type. The second from the left is European, but of Mediterranean origin, being actually made from a Sardinian skeleton. Nos. 45 and 184 are both Egyptian, the first representing Group "B" and the second Group "A." The Mediterranean column pairs better with No. 45, and the European with No. 184. The column on the right is included to show the type of the true Nordic in a Saxon column. Centimetre scales accompany these tracings.

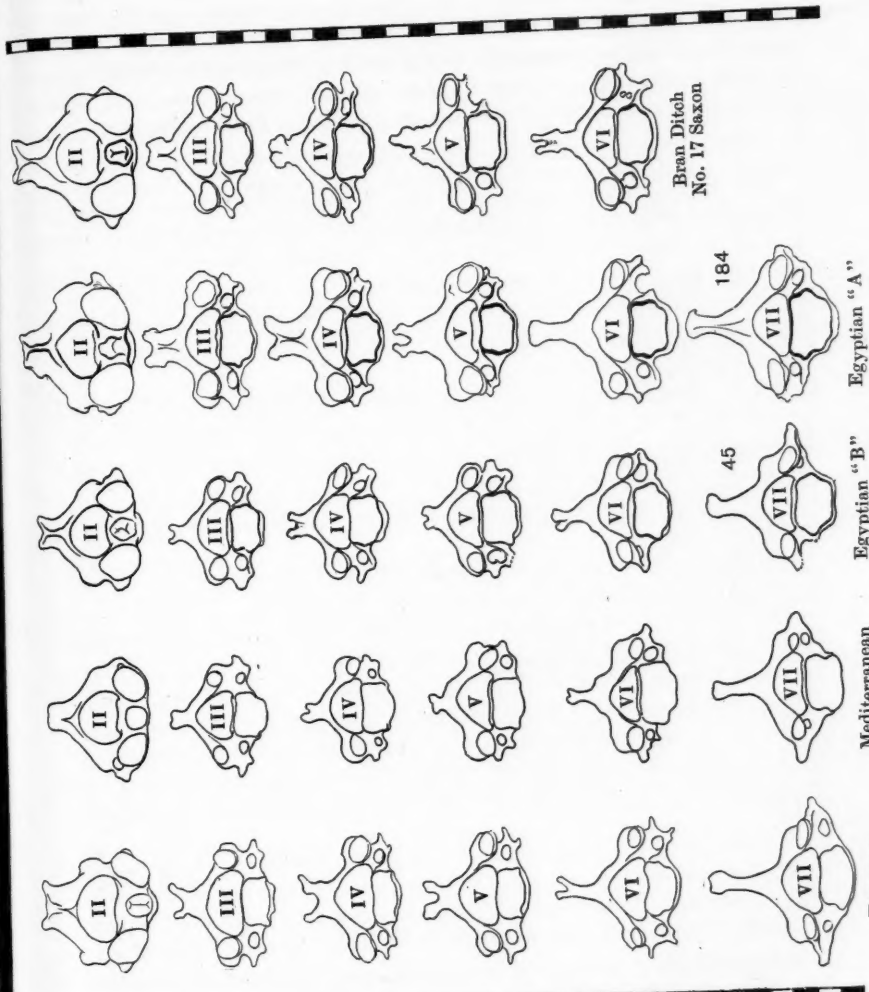

Fig. 3. (Scales in centimetres)

and from the ovoid dorsal extremity. In the main, this description applies to the prominent spinous process of the seventh cervical vertebra. It is to be inferred, therefore, that specimens of this type greatly exceed the others in length. Clavate spinous processes have been found constantly in the seventh, quite commonly in the sixth, and occasionally in the fifth cervical vertebra. Examples are shown throughout figs. 2 and 3 in the seventh vertebra.

Table II shows the proportions of the different types of non-bifid cervical spinous processes found in European, Egyptian and Bantu skeletons.

Discussion

The heteromorphous character of the type-content of the spinous processes in Egyptian cervical columns will be appreciated from the following statement. A set of the middle three cervical vertebrae possessing spinous processes of one type only was found in no more than 19 out of 58 columns. Of these 19, the bifurcate type accounted for 16, and the pediculate type for 3. In all the other Egyptian cervical columns more than one of the types described were mingled in the middle three units.

Of 71 Bantu cervical columns 20 presented a homogeneous type in the spinous processes of their middle members, a smaller proportion than in Egyptians. The type of 13 of these 20 was pediculate, of 3 acute and of 4 obtuse. A contrast is shown by European cervical columns, because out of 28 no less than 24 were uniform in presenting the bifurcate type of spinous process in the middle members.

Heteromorphism, then, is a feature of the type-content of the spinous processes of most Egyptian and Bantu cervical columns. It may be possible to trace an affinity between the two races in this respect. When heteromorphism is not present, the pediculate type is most common in Bantus, and in Egyptians the same type is alternative to bifurcate. A racial character shared by both Bantus and Egyptians in the pediculate type may be conjectured.

In the other report reasons were adduced to support the proposition that, in the Negroid races, the cervical spinous processes had entered upon a stage of regression. The non-bifid types have their counterparts in sub-human species.

The *clavate type* is predominant in the gorilla and in the orang, extending throughout the cervical column. The same type occurs in the chimpanzee, but is less consistent. Broadly speaking, the clavate type is anthropoid; and in this connection may be noted the tendency of this type to extend from the seventh vertebra upwards in the cervical column in all the races under our consideration (*vide* Table II and fig. 2).

The *pediculate type* is found in the gibbon and not commonly elsewhere in Primates except in the lemurs. The *acute type* is found in anthropoid apes and in some lemurs, but is most common in monkeys. The *obtuse type* seems to be sub-Primate in position. A complete set was found in a skeleton of *Didelphys cancrivora*, but in Primates, except in the axis, the type is uncommon.

Some little information is accumulating regarding the palaeontology of the Negroid races. It is indicated, so far as it goes, that the cervical spinous processes of fossil Man both in Africa and in Europe lacked the bifid character, and in addition were longer and more horizontally placed than in modern Man.

Laing and Gear (4) and Wells (5), working at the University of the Witwatersrand, have described these features in fossil Man found in South Africa. Duckworth (6), writing of the gorilla, states: "these spinous processes are not, however, bifid, and thus differ from those of existing human races of Europe, although approached in this respect by the cervical vertebrae of the primitive human races in other regions, and also the historic skeleton from La Chapelle-aux-Saints in France." Boule (7) gives a drawing of the La Chapelle vertebrae, from which I infer that the cervical spines from the fifth to the seventh are of clavate type.

A few observations on the form of the cervical spinous processes of Bantu foetuses, observations that I cannot pursue further, indicated that a change in the type of these structures, from bifid to non-bifid, takes place in post-natal development. Von Eggeling, in the paper to which I have already made reference, records studies in ontogeny which show that a like change takes place in the post-natal stages in the European cervical column also.

The history of Man's cervical spinous processes might be deduced from this scanty summary of variation, palaeontology and ontogeny to run somewhat as follows. Fossil Man had non-bifid cervical spinous processes; he acquired the bifid character in a post-primitive epoch; with the onset of regression, Man is now in the stage of losing the bifid character of his cervical spinous processes and of reproducing the types of lower animal forms. This third stage has made great progress in the Bantus and in some other Negroid peoples, and a little, though definite, progress in Europeans. The Egyptians, viewed in bulk, show an intermediate stage in this retrograde process.

That the cleft type may possibly be an early manifestation of this retrograde change, viz. bifid to non-bifid, may be suggested, but perhaps the point is not to be unduly stressed. The presence of anthropoid, of sub-anthropoid and of sub-Primate types among the cervical spinous processes is a more obvious indication of regressive change. That this change is well established is shown by the figures in Tables I and II.

V. BIFURCATE AND CLEFT CERVICAL SPINOUS PROCESSES

The need of a sub-classification of bifid spinous processes has been sufficiently emphasised and the sub-types have been defined. Cunningham was probably reluctant to add to terminology, but felt the need for more exact terms when he called "neural spines" by such names as "bifid" and "feebly bifid" in contradistinction to non-bifid in the paper already noted. Unfortunately some uncertainty as to this author's exact meaning remains. Comparing the neural spines of the second to the fifth vertebrae inclusive, Cunningham found the

following numbers in 15 European skeletons—bifid 43, feebly bifid 12, non-bifid 5; but the numbers in 24 skeletons of the "lower races" were respectively 26, 28 and 42. Hence it is deduced, non-bifid cervical spinous processes amounted to 43·8 per cent. in columns of the "lower races" and to 8·3 per cent. in those of Europeans under Cunningham's observations.

My observations for the same vertebrae, and expressed in a manner comparable to Cunningham's, show that non-bifid cervical spinous processes account for 42·5 per cent. in Bantus and for 7·5 per cent. in Europeans, which figures are very similar to Cunningham's, if the Bantus be accepted as representatives of the "lower races." The value for Egyptians is intermediate, viz. 28·7 per cent.

The reader is invited to consider the following short series of figures:

	European		Bantu or "lower races"	
	Cunningham	Writer	Cunningham	Writer
	%	%	%	%
(1) Non-bifid	8·3	7·5	43·8	42·5
(2) Bifid	91·7	92·5	56·2	57·5
(3) Ratio bifid to total of bifid plus "feebly bifid"	78·2	—	48·1	—
(4) Ratio bifurcate to total bifid (which includes cleft)	—	93·2	—	55·7

The ratios (1) and (2) are so similar that there is no doubt that Cunningham and the writer interpret "bifid" and "non-bifid" alike; but ratios (3) and (4) are so divergent that it is impossible to identify "bifurcate" with "bifid," or "cleft" with "feebly bifid." Probably "feebly bifid" includes spinous processes that are cleft as well as some that are bifurcate.

Cleft spinous processes occur in all the races of man yet examined but their significance is uncertain. For the following reasons I have considered them to be regressive or degenerate.

Cleft spinous processes have not been observed in complete series in the middle members of a cervical column, but have been observed in association with all the other types described. In Bantu skeletons they are found especially associated with bifurcate and pediculate types. In the Egyptian series the same is true; cleft types were found, disregarding the axis, in 5 columns; they accompanied bifurcate types in 2, pediculate types in 1, and mixed bifurcate and pediculate types in 2 columns.

If the suggestion be accepted that there is evidence of regression, that is, of reversion of type on the part of cervical spinous processes, as was very briefly discussed in Section IV, then it may be added that the proportion of cleft types to bifurcate is highest where evidence of that regression or reversion is most marked. This reversion is shown by the occurrence of non-bifid cervical spinous processes which are the counterparts of the like structures found in anthropoid, sub-anthropoid and sub-Primate mammalia. Table I shows that this is most marked in Bantu skeletons, in the non-bifid spinous processes, and so also it is with the cleft type.

The proportions of cleft to bifurcate, deduced from the data set out in Table III are as follows: in European columns 8 to 105, or 1 to 13·3; in Egyptian 1 to 14·3; and in Bantu 37 to 48 or 1 to 1·3. For these reasons I suggest that the cleft cervical spinous processes mark a stage on the retrograde path and, perhaps, in an evolutionary sense lie intermediate between the bifurcate and the pediculate types. I am not familiar with cleft cervical spinous processes in sub-human mammalia.

In Table III are set out the numbers of bifurcate and cleft cervical spinous processes found in the available skeletons of the three races under consideration.

Table III. *Bifurcate and cleft cervical spinous processes in European, Egyptian and Bantu skeletons*

		Vertebrae							
		II	III	IV	V	VI	VII	Totals	%
European	Bifurcate	19	24	26	26	10	0	105	62·87
	Cleft	5	0	1	1	1	0	8	4·79
	Other forms	4	4	0	1	17	28	54	32·33
	Totals	28	28	27	28	28	28	167	
Egyptian	Bifurcate	16	25	38	42	22	0	143	43·46
	Cleft	4	1	1	2	2	0	10	3·04
	Other forms	24	32	19	14	34	53	176	53·50
	Totals	44	58	58	58	58	53	329	
Bantu	Bifurcate	9	6	11	13	9	0	48	11·94
	Cleft	8	3	6	14	6	0	37	9·20
	Other forms	53	58	48	38	55	65	317	78·85
	Totals	70	67	65	65	70	65	402	

VI. DIFFERENT FORMS OF BIFURCATE CERVICAL SPINOUS PROCESSES

The type of cervical spinous process which is most familiar to those who studied Anatomy in a British school with a British textbook is robust and broad-based and has dorsal segments that diverge boldly. It is peculiarly to this type that the name of "bifurcate" applies, being as it is in harmony with the general use of that word in Anatomy.

It has been previously remarked than in skeletons from Sardinia and from South Africa the average bifurcate cervical spinous process is less robust and less conspicuously bisected, and that the lateral alae are shorter and the angle of their divergence is smaller. The type found in skeletons of Northern European origin is more robust and is unequivocally bifurcate. These descriptions were previously used to indicate two groups, seemingly anthropological groups, of skeletons to which the names "Nordic" and "Mediterranean" were given.

I have no wish to stress the implication of the terms "Nordic" and "Mediterranean," that crept into my other report, more strongly than the facts justify. I have been unable to extend my knowledge of the cervical spinous processes of the peoples of the Mediterranean littoral. The Museum of the Royal College of Surgeons possesses but one cervical column (No. 6·039)

from the Moslem Cemetery, Safad, Galilee, probably Turkish. Prof. Elliot-Smith informs me that University College possesses no Mediterranean columns other than Egyptian and there are none at Cambridge.

Wider examination of Northern European skeletons rather confirms my opinion of the "Nordic" type. However, to avoid begging the question, I propose to describe two sub-types of bifurcate cervical processes thus:

Type A. Robust, broad-based, strongly bifurcated.
Type B. Slender, narrow-based, less definitely bifurcated.

The reader is now invited to examine the tracings in figs. 2 and 3. In fig. 2, the column on the right, No. 151, shows bifurcate spinous processes of Type "B," though the columns in this figure were selected in order to illustrate different types of cervical processes, rather than variations of the bifurcate type. The tracings in fig. 3, however, may be viewed from the comparative aspect. The column on the left will be generally accepted as typical of the Northern European skeleton, with robust and broad-based spinous processes and bold bifurcation. The next from the left is a column from Sardinia and exhibits spinous processes of the bifurcate sub-type I previously called "Mediterranean." These two columns will serve to illustrate the essential differences between the two forms that European bifurcate cervical spinous processes may take, and to explain certain passages in the Introduction.

The third column from the left, No. 45, is representative of the Egyptian Group "B," and the column on its right, No. 184, of Egyptian Group "A." It is evident that the European column on the extreme left and No. 184 pair together, in the same way as do the Sardinian column and No. 45, in respect of build, of width of base and of character of bifurcation.

The reader will understand that it was not a difficult matter, when surveying the Egyptian cervical columns, to set on one side those that presented the more robust characters of Group "A." The whole Egyptian material was so rendered into two Groups "A" and "B." No cervical column was placed in Group "A," unless the characters of robust growth with broad base and decisive divergence of the segments were satisfied in its spinous processes. No doubt, this classification is rough; intermediate forms and columns of mixed characters occur. All such were referred to Group "B"; but using the classification for what it is worth, interesting results emerge.

Table IV shows the numbers of bifurcate, cleft and non-bifid spinous processes found in the cervical columns of each of the three groups: (1) Egyptian Group "A," (2) Egyptian Group "B," (3) European skeletons.

Group "A" contains 21 cervical columns, Group "B" 37, and, as previously stated, the European group contains 28 columns.

Table IV shows that the proportion of bifurcate cervical spinous processes is far higher in the columns of Group "A," of robust characters, than it is in Group "B," whose columns are slender or mixed—60 per cent. as compared with 34 per cent. In Bantus the value is about 12 per cent.

The figure for Group "A" is slightly smaller than for the European group in respect of bifurcate cervical spinous processes, while that for cleft is greater in the European group.

The columns in fig. 3 have been explained with the exception of that on the right. This column corresponds closely in form to No. 184 and to the European column on the left. In point of fact this column is the most complete of those previously referred to as Saxon, having been recovered from the Bran Ditch at Melbourn in Cambridgeshire, and has been included to show the characters of a true Nordic cervical column. It is perhaps unfortunate that the sixth spinous process is cleft in type, being indeed the only cleft specimen of the sixth vertebra in the European series. The other vertebrae have spinous processes of definitely robust type, and the presence of this cleft member is less to be regretted if it serves as a reminder that the type does occur in Europeans.

Table IV. *Bifurcate, cleft and non-bifid cervical spinous processes in the columns of* (1) *Egyptian Group "A,"* (2) *Egyptian Group "B," and of* (3) *European skeletons.*

		Vertebrae							
		II	III	IV	V	VI	VII	Totals	%
Egyptian Group "A"	Bifurcate	7	16	20	19	9	0	71	60·16
	Cleft	1	0	0	0	0	0	1	1·85
	Non-bifid	8	5	1	2	12	18	46	38·98
	Totals	16	21	21	21	21	18	118	
Egyptian Group "B"	Bifurcate	9	9	18	23	13	0	72	34·12
	Cleft	3	1	1	2	2	0	9	4·26
	Non-bifid	16	27	18	12	22	35	130	61·61
	Totals	28	37	37	37	37	35	211	
European	Bifurcate	19	24	26	26	10	0	105	62·87
	Cleft	5	0	1	1	1	0	8	4·79
	Non-bifid	4	4	0	1	17	28	54	32·33
	Totals	28	28	27	28	28	28	167	

However, it is submitted that the European columns on the right and on the left provide the best match for the column No. 184, set out in fig. 3 as typical of Group "A."

It is not only in the form of their bifurcate cervical spinous processes that the columns of Group "A" stand out, nor in the frequency of occurrence of that type, but conspicuously in the relative homogeneity of the type-content.

In 21 cervical columns, assigned to Group "A," there are 15 of which all the middle members (III, IV, V) present the characteristic bifurcate form in their spinous processes. The sixth member is also bifurcate in 4 of this 15, and the axis is bifurcate in 5 of these columns. On the other hand, 37 columns of the contrasting Group "B" provide only one column whose middle members all present the bifurcate type in their spinous processes. This column, No. 45, is shown in the middle of fig. 3, and it will be seen in addition that bifurcate spinous processes are present in the axis and in the sixth vertebra; moreover

the whole column is a fair match for the Sardinian column marked "Mediterranean" in fig. 3.

If the range of our observation be extended from the third to the fifth, so as to include the sixth vertebra, even then a content of three bifurcate spinous processes is found in only 5 columns out of 36. Of the remaining columns of Group "B," 16 contain two bifurcate spinous processes, and 15 less than two. In short, the great majority of the columns that compose Group "B," 36 out of 37 exhibit a variety of forms in their spinous processes or, as I have called it, heteromorphism in their type-content. This character is reminiscent of Bantu cervical columns, as also is the slender type of bifurcate spinous process (*vide* Introduction).

The inference to be drawn from these findings is unavoidable; we are dealing with two separable racial groups in these skeletons of early Egypt.

It might be suggested that the skeletons with the robust type of cervical spinous process, Group "A," belong to strangers possessing a strong strain of the characters that I have elsewhere provisionally called "Nordic." On the other hand, the Egyptian Group "B," on account of the similarity with the Sardinian would seem to belong to some native race of the Mediterranean. But, whoever this people may be, they seem to show some affinities with the Bantus also. They may be hybrids between Mediterranean peoples and Bantus or forerunners of the Bantu peoples.

The cervical column in the Museum of the Royal College of Surgeons (No. 6·039) from Safad, Galilee, is of mixed type-content. The spinous processes of the five middle members all exhibit the bifurcate character, though the fourth spinous process has the characters of Group "A," the others rather resemble Group "B." The whole column I would refer to Group "B."

Whether or not the skeletons in which I [illegible] resemblances to those of Nordic peoples in the cervical spinous p[illegible]esses, a[illegible] indeed Nordic, is a question that cannot be answered in the present state of knowledge. The name was applied in a speculative way to indicate a certain resemblance and had a certain convenience. Much wider information is required on the condition of the cervical spinous processes of the peoples not only of the Mediterranean and of the North, but also of Asia Minor and of Middle Europe. All that can be stated is that the cervical spinous processes of Nordic skeletons provide a good match for the like structures of an anthropological group that can be isolated from the Egyptian medley.

From the outset, the facts of geography present a difficulty in identifying this group with true Nordics. It is improbable that Northern mercenaries, settlers or slaves could have contributed so large a share to the community of Egypt in predynastic days. There may have been a common root-stock of men who peopled Northern Europe, perhaps from Asia Minor, and took a share in the population of Egypt also. These people, perhaps, have in some measure left the mark on the Egyptians of the cervical columns proper to the Northern peoples.

I have less hesitation in suggesting that the Negroid peoples of Africa took a share in populating Egypt. These are weighty propositions to support on pegs no longer or stronger than are the spinous processes of the cervical vertebrae.

VII. THE FORM OF THE SPINOUS PROCESS OF THE AXIS VERTEBRA

Fig. 4 represents scale-drawings of the Egyptian axis, made by the aid of the dioptograph, in both norma verticalis and norma dorsalis. The drawings of each specimen are set out in the same way, with the view in norma verticalis above that in norma dorsalis, and are accompanied by a centimetre scale.

The axis of common description and the form represented in British text-books has divergent alae when viewed in norma verticalis and when viewed in

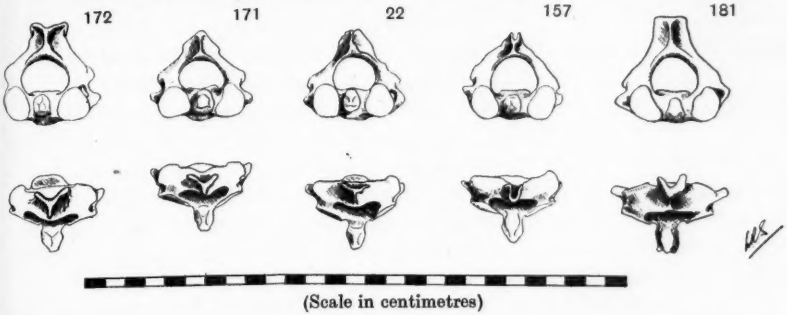

Fig. 4. In this figure are shown scale drawing of five specimens of the axis vertebra, all Egyptian, viewed in both norma verticalis and in norma dorsalis. The view in norma verticalis is set above the view in norma dorsalis for each specimen. No. 172 is bifurcate and of inverted *Y* form; No. 171 and No. 22 are both obtuse but the former is of *V* and the latter of *T* form; No. 157 is cleft and of *U* form; 181 is flat topped and of *U* form. The scale below the drawings represents centimetres.

norma dorsalis presents the appearance of an inverted *Y*. This form is shown in No. 172, on the left of fig. 4. In this figure the axis has been placed with the odontoid process pointing downwards, i.e. with the bone reversed. The consequence is that the *Y* is now the right way up. This arrangement may make it easier for the reader to follow the descriptions that follow, in which the form of the spine of the axis has generally been compared to an alphabetical symbol; but the fact of inversion must be borne in mind.

Variations of the *Y* form occur frequently; the median ridge may be lacking and an inverted *V* form results (No. 171, fig. 4); the alae may diverge excessively and give rise to a *T* form (No. 22, fig. 4); or divergence may be slight and an inverted *U* may be substituted for *Y*, *V* or *T* (No. 157, figs. 4). Bifurcate and cleft forms occur in various combinations with the forms found in norma dorsalis. Not uncommonly the spinous process in norma verticalis is neither bifurcate nor cleft, but squarish and flat topped (No. 181, figs. 4). Obtuse forms have been represented in fig. 2 (Nos. 193 and 151).

The 21 columns of Egyptian Group "A" furnished 16 specimens of the axis, and the 37 columns of Group "B" 28 specimens. The combinations of the forms observed are recorded in Table V.

The forms that are flat or obtuse in norma verticalis are regarded as non-bifid in that norma, and *T* forms are regarded as non-bifid in norma dorsalis.

In all three groups bifurcate *Y* and *V* forms are common. The spine of the European axis is bifid in one norma or the other in all, and in both normae at once, in 24 out of 28 specimens.

Egyptian Group "A" shows 10 out of 16 bifid in both normae at once, and Egyptian Group "B" 15 out of 28, which is a much smaller proportion. Though non-bifid flat forms constitute a small proportion of each total, obtuse forms are present in every group and form an especially large proportion of the total

Table V. *The form of the spinous process of the axis vertebra in skeletons of* (1) *European,* (2) *Egyptian Group* "A," (3) *Egyptian Group* "B."

		Norma dorsalis Inverted				
	Norma verticalis	*Y*	*V*	*U*	*T*	Totals
European (28 columns)	Bifurcate	9	7	3	0	19
	Cleft	1	1	3	0	5
	Flat	1	0	0	0	1
	Obtuse	2	1	0	0	3
	Totals	13	9	6	0	28
Egyptian Group "A" (21 columns)	Bifurcate	6	2	0	0	8
	Cleft	0	1	0	0	1
	Flat	2	0	1	0	3
	Obtuse	1	0	0	3	4
	Totals	9	3	1	3	16
Egyptian Group "B" (37 columns)	Bifurcate	6	3	0	0	9
	Cleft	1	1	1	0	3
	Flat	1	2	0	0	3
	Obtuse	6	6	0	1	13
	Totals	14	12	1	1	28

in Egyptian Group "B." In the series of Bantu specimens surveyed elsewhere, only 16 out of 70 specimens were bifid in both normae at once. Flat-topped and obtuse spines together formed 53 out of the total of 70; the obtuse form being in distinct excess of the flat-topped.

It is of interest to recollect that Macalister (8) noted the lack of the median ridge of the spinous process of the axis (*V* and *U* forms) in 2 per cent. of axes, and regarded this character as the persistence of a feature of immaturity. Macalister noted forms in the axis of Egyptians, apparently obtuse in both normae, to judge from the name he applied, "acuminate." This form has been met by the present writer in Bantus, but not in this Egyptian series. Macalister remarked, by way of contrast, on the great intertubercular width in certain specimens of the axis of Saxon skeletons from Bowl's Barrow, Wilts.

VIII. SUMMARY AND CONCLUSIONS

A survey has been made on the form of the cervical spinous processes of 58 Egyptian skeletons, dating from predynastic times and from those of the earliest dynasties; and a comparison has been made between these and the like structures in 28 European and 71 Bantu skeletons.

The "bifid" character of the cervical spinous processes, the atlas excepted, accounts for 67·6 per cent. in the European, for 46·5 per cent. in the Egyptian and for 21·2 per cent. in the Bantu columns.

Sub-varieties of "bifid" cervical spinous processes are described. Those having divergent segments are named "bifurcate" and those with parallel segments "cleft." Non-bifid cervical spinous processes resemble forms found in anthropoid, sub-anthropoid and sub-Primate mammalia and are given names suggested by their appearances in norma verticalis. The cleft form is considered to be regressive and is found in most frequent association with non-bifid forms, i.e. in the Bantu skeletons.

Bifurcate cervical spinous processes may be robust, broad-based and boldly bifurcated, or they may be slender-based and feebly divided.

The Egyptian cervical columns have been divided into two groups on the basis of these qualities in their spinous processes. The columns with robust, broad-based bifurcate spinous processes account for 21 out of 58 columns, called Group "A" in this report; the other 37 columns contain the more slender, the less definitely bifurcated spinous processes and those mixed or uncertain in their characters, called here Group "B."

Group "A" columns possess cervical spinous processes of the bifurcate type in far greater numbers and far more consistently than do those of Group "B." The columns of Group "B" have fewer spinous processes of the bifurcate type, many more of non-bifid types and many columns of mixed type-content as regards the spinous processes of their middle members.

In Egyptian Group "A" the content of bifurcate cervical spinous processes, expressed as a percentage of the total, almost equals that of the European group. In this respect the Egyptian Group "B" is lower than Group "A," but higher than the Bantu.

The non-bifid types found in Egyptian columns, mainly in Group "B," resemble those found in the Bantu. Further resemblance is found in heteromorphism within the individual columns and in the presence of the pediculate type.

The bifurcate types of Egyptian Group "B" resemble the bifurcate types of a group of columns from Sardinia and perhaps are representative of the Mediterranean littoral; they also resemble a majority of bifurcate types found in Bantus. The bifurcate cervical spinous processes of Egyptian Group "A" find a good match in those of Nordic skeletons.

In the European columns all specimens of the axis had spinous processes which were bifid in one norma or the other, and 24 out of 28 in both normae.

The spine of the Egyptian axis is bifid in norma dorsalis hardly less commonly than in the European. Forms that are bifid in norma verticalis are rather more commonly met in the robust Egyptian Group "A" than in the slender Group "B" (9 out of 16 compared with 12 out of 28). Forms obtuse in norma verticalis are not lacking in European columns and are little more common in Egyptian Group "A," but in Egyptian Group "B" they account for almost half the total as they do in Bantu columns. The spines which appeared flat topped in norma verticalis so commonly in Bantu columns are far fewer in Egyptian columns.

The question if a true Nordic strain exists in 21 out of 58 skeletons of ancient Egypt must remain open for the present. Geographical considerations present a difficulty; but it might be suggested that the root-stock that peopled Europe from Asia Minor and the root-stock of the Bantus both have had a share in populating Egypt.

IX. ACKNOWLEDGMENTS

It is a great pleasure to acknowledge the kindness of Prof. J. T. Wilson and of Dr Duckworth, who gave me a welcome to the Anatomy Department at Cambridge and allowed me access to the Museum with facilities for research. Dr Duckworth, in addition, by discussion of certain points and by reading this paper in draft form has done me a service that I acknowledge most gratefully.

The tracing shown in fig. 3 above the title "Mediterranean" is one of several made by myself in Johannesburg from the Sardinian skeletons in the Anatomy Museum. I gratefully acknowledge my indebtedness to Prof. R. A. Dart and to the Anatomy Department of the University of the Witwatersrand.

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THE ANATOMY OF THE HEAD OF *CALLORHYNCHUS ANTARCTICUS*

By H. LEIGHTON KESTEVEN, D.Sc., M.D., Ch.M.Syd.

It is not proposed to describe completely, or in detail, the anatomical features of the head, but only to deal with those portions of the arrangement and relation one to the other of the skeletal, muscular, vascular, and nervous systems, which past experience has shown to be of prime importance to the student of phylogeny.

EXTERNAL FEATURES

(Plate I, figs. 1 and 2)

One notes first, the absence of the spiracles and the possession of a membranous and cartilage-supported operculum which carries on its inner side the first hemibranch and forms the outer wall of the branchial pouch, which is gathered under the head as in the teleostomes.

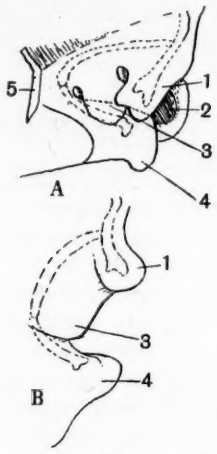
There are two skin folds above the upper jaw and one around the lower. The upper of the two superior folds, the *velum* (Plate I, fig. 1), commences in front at the root of the rostral process on each side and passes directly back to the angle of the mouth. Of the second superior fold Parker and Haswell (1897, p. 174) significantly remark that they are supported by labial cartilages, and "resemble the folds in which the premaxillae and maxillae of the bony Fishes are enclosed."

The "lip" of the lower jaw is strengthened by a large leaf-shaped cartilage.

The nasal aperture is incompletely divided by a flap of skin containing a squame of cartilage (middle nasal cartilage), into upper and lower apertures. The partition is attached to the edge of the nasal septum and its free edge lies against the inner side of the outer wall of the aperture it divides (Plate I, fig. 2).

The lips call for detailed description. The upper, double "hare-lip" in form, when closed presents two folds. The anterior fold is thick and forms the outer boundary of the nasal aperture. It rises above from the nasal septum and arches out and down (Plate I, fig. 2). This anterior fold has within it the lower portion of the anterior of the two superior labial cartilages. The posterior fold of the upper lip lies behind the other, overlapped by it when closed. In this position the two folds are separated by a sulcus, and a shallower sulcus separates the posterior fold from the lower lip. The posterior superior labial cartilage lies in the upper lip above the two sulci. The posterior sulcus is the angle of the closed mouth, and the posterior superior labial cartilage ends

just above and behind the inner end of this sulcus, joining the small inferior labial cartilage in this situation. The lower lip also presents two parts. The first is a thin fold which lies internal to the posterior fold of the upper lip, joining this to the outer aspect of the main part of the lower lip well towards the anterior end. The main portion of the lower lip is a very thick fold of skin, containing the large lower labial cartilage, which is losely attached to the outer aspect of the lower jaw. The lower portion of the small inferior labial cartilage is enclosed in the small component of the lower lip, passing down to this position on the inner side of the lower portion of the posterior fold of the upper lip.



Text-fig. 1. To show the manner in which their skeletal framework moves with the lips. 1, anterior fold of the upper lip. 2, septum nasi; supported by the median nasal cartilage. 3, posterior fold of the upper lip. 4, lower lip. 5, velum, cut and folded back.

In text-fig. 1 I have indicated the position of the lips and their cartilaginous skeleton with the lips closed and open. It is of particular interest that these lips are not only supported by a special framework, but are capable of being opened and closed independently of the jaws by a special set of muscles.

THE CRANIUM

(Plate II, figs. 3 and 4)

The most striking feature about the cranium is the situation of the orbit far towards the posterior end; this produces the impression that the quadrate-Meckelian joint is far forward. This latter is a fact, but it is not so far forward as it appears to be.

Behind the orbit the cranium is broadened by the otocranes, but the hind wall of the orbit stands out further than these capsules. In front of the orbit

the cranium is markedly compressed and surmounted by an expansive vertical crest. The base of this crest is tunnelled (Plate II, fig. 4, *Oph.*) for the transmission of the two ophthalmic nerves. Below the canal for these nerves lies the sphenoidal division of the cranial cavity. A vertical partition divides this anteriorly into the two olfactory passages.

The orbit is provided with complete roof, posterior wall, and floor, and is overhung in front by an incomplete front wall.

In front of the orbit the sheet of cartilage that forms its floor is continuous with the quadrate (?) and this with the side and floor of the sphenoidal cavity and palatine expansion beneath the olfactory passages. Whereas the floor of the orbit is nearly horizontal the sheet of cartilage which connects the quadrate to the cranium slopes sharply down.

Just in front of the anterior aperture of the ophthalmic canal the rostral spine is attached. This "spine" is a fibrocartilaginous structure; below it a pair of little spurs project (Plate II, fig. 4) towards the roof of the nasal capsule from the sagittal crest.

The outer boundary of the anterior aperture of the ophthalmic canal on each side is lifted as a ridge and then produced into a short spine, post-nasal spine (Plate II, fig. 4). This marks the posterior and upper limit of the nasal capsule. The roof, outer wall, and half the floor of the nasal capsule are formed from a curved sheet of cartilage which springs from the sagittal crest beside and just in front of the rostral spine, and arches round to be attached below. There is also contributing to the roof a little squame which is continuous with the spur above described, and fits under the fore and upper corner of the roof, and is bound thereto by strong fibrous tissue.

There are two accessory nasal cartilages. The first (median nasal cartilage) continues the floor and medial wall forward; in shape it may be compared to the front half of a little spoon. It is attached to the sagittal crest in front of the anterior limit of the capsule. To the upper and median edge of this there is attached a little squame, inferior nasal cartilage, which, projecting out and downward, forms a roof, as it were, to the hollow of the median nasal cartilage. This little squame reaches the outer edge of the median nasal cartilage but is not attached thereto. It divides the nasal aperture into a larger upper and smaller lower part.

The cartilaginous support of the upper lip is quite a complex little structure; five separate pieces enter into its formation. The anterior piece (Plate II, fig. 3, *A.c.*) is the largest, its shape as seen from the side is shown in the drawing. The lower portion is flattened and spread out in the margin of the upper lip in front. Higher up, in the thicker part of the "hare-lip," the cartilage thickens, and then presents a flattened surface as seen from in front, beside, lateral to, the nasal aperture. Above its point of articulation with the middle piece it becomes fibrocartilaginous and is bound to the lateral tendon of the rostrum, just as that turns down to reach the post-nasal spine. The shape and position of the middle piece (Plate II, fig. 3, *P.c.*) are well shown in the

drawing. This, where it joins the anterior piece, lies underneath the velum at some distance from the margin of the mouth, but approaches more nearly to the margin as it passes downward and backward towards the angle of the lips. The inferior piece (Plate II, fig. 3, *S.i.c.*) lies along the upper margin of the lower lip, its spathulate end is firmly bound to the skin of the lip and fore-end of the large lower labial cartilage. This framework is attached to the cranium above and below the nasal aperture by other two cartilages. The first of these is a tiny splinter interposed between the upper end of the anterior piece and the sagittal crest, to which it is bound along with the median nasal and inferior nasal cartilages. The fifth cartilage (Plate II, fig. 3, *S.c.*) is a curved cylinder which is situated in the outer boundary of the nasal aperture. It is attached to the inner side of the anterior piece just below the junction thereof with the middle piece. The deep end is planted very firmly in a little pit just in front of the nasal floor.

The inferior labial cartilage (Plate II, fig. 3, *L.i.c.*) is a large, flattened, leaf-like plate placed in the lower lip and loosely bound to the outer surface of Meckel's cartilage. The two large inferior labial cartilages are bound together around the front of the symphysis of the lower jaw by firm, compact, connective tissue, the transition from cartilage to this connecting tissue being so gradual that it is impossible to state where the one begins and the other ends.

In the description of the lips the anterior and middle pieces have been regarded as anterior and posterior upper labial cartilages and the posterior as the posterior lower labial cartilage. This, I believe, is the correct identification of the pieces.

The cranial cavity, and the nerve and vascular foramina

The shape of the cranial cavity is clearly shown in Plate II, fig. 4. The olfactory lobes lie in an elongated sphenoidal compartment of the cavity, the peduncles are quite short, reaching the organ through a widely open passage.

There are two large deficiencies in the cartilaginous side wall of the cavity. The extent of the orbital deficiency is indicated by an interrupted line in the drawing; this is made good by a very strong (sphenoptic) membrane. The otic deficiency is made good by a delicate membrane, of which it has been found impossible to define the limits. Actually portions of the labyrinth appear to lie in the side of the cranial cavity supported by loose connective tissue.

The optic nerves perforate the sphenoptic membrane low down close to the anterior margin.

The third nerves perforate the cartilaginous wall at the hinder margin of the sella, just behind the membrane.

The fourth nerve perforates the sphenoptic membrane a little higher than is shown in the drawing.

The fifth and seventh nerves leave the cavity through two foramina. The upper of these foramina transmits the ophthalmic branch only of the seventh

nerve. The lower and larger, funnel-shaped, foramen prooticum, is divided by fine cartilaginous strands into four divisions.

The sixth nerve perforates the floor of the cavity immediately behind the sella.

The eighth nerve proceeds direct to the various parts of the otic labyrinth.

The ninth nerve leaves the cavity through a little foramen close to the floor.

The foramen for the tenth nerve is close behind that for the ninth.

The external apertures of all these nerve foramina, except those for the first, eighth, ninth, and tenth, are actually within the orbit (text-fig. 3).

A fine canal for the cerebral artery passes from the depth of the sella turcica on each side to the orbit.

The auditory capsule

(Text-fig. 2)

Although the three semicircular canals make their presence evident on the outer surface of the skull by corresponding ridges, the capsule is, as it

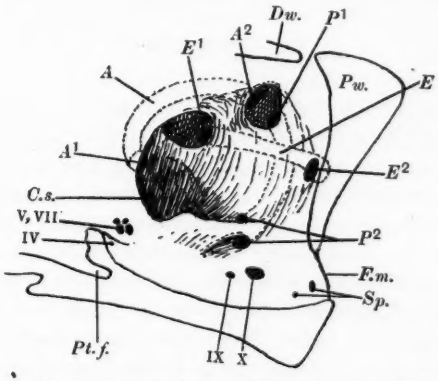


Fig. 2. The otic region of the inner wall of the cranial cavity. *A*, anterior vertical semicircular canal. A^1, its ventral, A^2, its dorsal aperture. *Dw.* cranial roof. *E*, the horizontal semicircular canal, E^1, its anterior, E^2, its posterior aperture. P^1, and P^2, dorsal and ventral apertures of the posterior vertical semicircular canal. *C.s.* cavum saculi. *F.m.* foramen magnum. *Pw.* posterior cranial wall, in section. *Pt.f.* sella turcica. *Sp.* spinal nerve foramina. V, VII, foramen prooticum. IV, foramen pathetici. IX, foramen glossopharyngei. X, foramen vagi.

were, so neatly packed in behind the orbit that one does not realise its extent till it is examined from within. The deficiency in the inner wall, lateral cranial fenestra (Kesteven, 1926), is so large that quite a large portion of all the chambers is visible through it. The cava saculi and utriculi are almost devoid of inner wall, only the lower portion of the former being separated below from the cavum cerebri. The cavum saculi is defined from the utricular area above it only by a low eminence which crosses the outer wall from in front, below

the inferior opening of the anterior vertical canal, backward and downward and finally mediad to just in front of the inferior aperture of the posterior vertical canal. In the depth of the upper forepart of the utricular recess the ventral aperture of the anterior vertical canal is seen, with the anterior opening of the horizontal canal behind and a little above it. The inferior opening of the posterior vertical canal lies in the utricular recess level with the cranial floor, imperfectly separated from the cranial cavity by a bar of cartilage medial to it. The posterior aperture of the horizontal canal is situated above and behind this last, appearing to open into the cranial cavity in the angle between side and posterior walls. The recess for the common stem of the superior ends of the vertical canals is above the last aperture and a little in front of it. I have endeavoured to depict the course of the three canals in the cartilage behind with dotted lines.

The crus communis of the two vertical canals and the posterior end of the horizontal membranous canal lie freely in the cranial cavity, joining the utriculus, which also is separated from the brain by loose connective tissue only.

The cartilaginous, common, foramen endolymphaticum is a remarkable funnel-shaped recess in the cranial roof.

The orbital cavity

(Text-fig. 3)

The orbital cavity externally has a quadrilateral outline, or perhaps it were better likened to a triangle with a truncated apex. The base of the triangle is anterior, the truncated apex, posterior. The inner wall, however, is triangular, with the same base, and the apex posterior and inferior. The change in outline is brought about by the gradual extinction of the angle between roof and posterior wall as the inner wall is approached. At the antero-dorsal angle of the inner wall there is a large foramen through which the ophthalmic nerves reach the ophthalmic canal below the sagittal crest. This canal is common to the nerves of both sides, which run forward side by side. The canal is deeper and wider behind than in front. The anterior aperture of the canal is crossed in the mid-sagittal plane by a laterally flattened bar of cartilage which divides the aperture into right and left halves.

At the postero-inferior angle of the inner wall there are four small foramina grouped together, so that they are divided from each other by quite fine bars of cartilage; these are the foramina of exit of the branches of the fifth and seventh nerves, except the superficial ophthalmic branch of the seventh. The foramen of exit of the superficial ophthalmic nerve is directly above it on the hinder wall of the orbit, just where the inner and hinder walls merge. Below and in front of the trigemino-facialis foramen, close to the floor, there is a foramen for the internal carotid artery on its way to the pituitary fossa. The little foramen for the otic branch of the external carotid artery is situated below and lateral to the foramen ophthalmicum. The sphenoptic membrane fills an irregular area in the inner wall. The foramen oculomotorius is situated

in the cartilage just below the postero-inferior angle of this membrane. The abducent foramen just above the last penetrates the edge of the membrane, whilst the pathetic foramen perforates the membrane high up. The optic foramen perforates the membrane at its antero-ventral angle.

On the floor of the orbit, the hyomandibularis foramen is placed far back and towards the inner side, and the anterior foramen for the ophthalmicus profundus branch of the trigeminus nerve is just above the floor at the antero-inferior angle of the wall. A foramen situated medial to the hyomandibularis foramen is for the palatine branch of the facial nerve and the internal carotid artery.

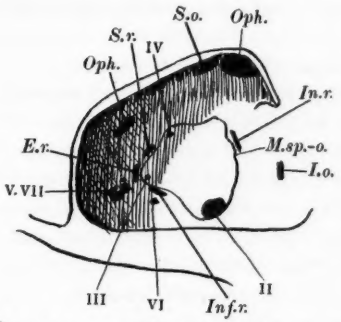


Fig. 3. The orbital cavity. The points of origin of the six ocular muscles. *E.r.* external rectus. *I.o.* inferior oblique. *In.r.* internal rectus. *M.sp.-o.* membrana spheno-obturatoria. *Inf.r.* inferior rectus. *S.o.* superior oblique. *S.r.* superior rectus. *Oph.* foramen ophthalmici and posterior aperture of the ophthalmic canal. II, III, IV, V, VII and VI, nerve foramina.

THE CRANIAL NERVES

It was naturally assumed that the cranial nerves of *Callorhynchus* would be very similar to those of *Chimaera*, therefore the dissection of these nerves was carried out with Cole's account (1896) before me. So close is the resemblance that in all essential points, as far as one may judge of what is essential, Cole's account describes the cranial nerves of both forms.

The following account will therefore be regarded as supplementary to Cole's, and will have to be read in conjunction with that description. It is supplementary because it does not repeat the account he gave, but notes only those differences observed, and gives the origin of the various motor nerves, and the relation of the main trunks and rami to the muscular and skeletal structures where Cole omitted to do so.

The roots of the cranial nerves agree absolutely with the illustration of the roots of those of *Chimaera* as given by Johnston (1907, p. 23). In other words I find the roots of nerves five, seven, eight, nine, and ten to be placed more dorsally than Cole indicated; in all probability Cole was in error in these particulars, and the two forms are really similar.

The *Trigeminus* and *Facial Nerves* (text-fig. 4). The ophthalmicus pro-

fundus branch in *Callorhynchus* can be definitely stated to arise from the anterior aspect of the trigeminus root, for the nerve maintains its identity and can be traced right back to the origin without much difficulty. It leaves the cranial cavity through the most anterior and median of the four fenestrations of the foramen prooticum, and in so passing is unaccompanied by any other nerve. The two branches to supra-orbital sense organs are not given off till after the nerve has penetrated the anterior wall of the orbit, and they then come off together and pass straight to their destination without again entering any cartilage. In front of the departure of these twigs the nerve penetrates the outer wall of the ophthalmic canal. Within the canal the nerve maintains its identity and can be very readily separated from the ophthalmicus superficialis of the facial nerve till after it has emerged again from the canal and passed under the ligamentum radicis rostris.

I have not found the superficial ophthalmic branch of the fifth nerve.

The maxillary and mandibular branches of the fifth nerve cross the floor of the orbit below all the ocular muscles along with the buccal division of the seventh nerve. The trigeminal branches lie *medial* to the buccal nerve. As the orbit is crossed the nerves broaden out and the buccal and mandibular nerve come towards the surface, the former overlying the latter. Their situation then is upon the surface of the ribbon-like levators of the upper and lower lips and rostrum, and beneath the velar muscles.

As soon as the anterior wall of the orbit is reached the buccal nerve commences to break up into a fan of twigs which spread both upward and downward and perforating the deeper tissues of the rostrum are distributed to the sense organs both above and below the orbit. The first of these branches are given off within the orbit and penetrate the fibrous anterior wall separately and turn backward to reach organs above the orbit.

The maxillary division of the trigeminal nerve runs forward under the main stream of the buccal branches, and its terminal fibres end on the surface of the muscles beneath it. Branches to the adductor mandibulae are given off within the orbit and reach the muscle deeply.

The buccal division of the facial nerve does not divide into inner and outer rami as in *Chimaera*.

The mandibular division of the fifth nerve leaves the orbit deeply in the valley between the two heads of the adductor mandibulae muscle. It gives off a number of twigs deeply to that muscle, some three or four of which turn downwards to supply the small posterior head of the muscle. The nerve comes to lie upon the same ribbon-like muscles as the maxillary division at the anterior end of the valley between the two heads of the adductor, and continues forward to the angle of the mouth. A communicating branch to the external mandibular division of the hyomandibular trunk is given off here and it then divides into two. One of these divisions breaks up on the inner face of the large lower labial cartilage, the other turns upward along the antero-inferior border of the superior protractor of the lower lip, and, passing

under the small inferior labial cartilage, was traced to the deep surface of the protractor of the upper lip. This is the motor nerve to these two last muscles, but doubtless it also carries general cutaneous sensory components.

The ganglia of the buccal and hyomandibular divisions were dissected apart only with great difficulty, and it was then found that there was a communicating branch from the former to the latter beyond the origin of the palatine nerve. Only two roots for the seventh nerve were found. This is in accord with Johnston's illustration, but one short of Cole's finding.

I have been unable to follow Cole's description of the hyomandibular trunk of the facial nerve, and have therefore reluctantly applied a different nomenclature to the branches, rather than cause confusion by the incorrect application of his names.

The palatine branch is given off first from the antero-lateral corner of the ganglion; it leaves the orbit through a foramen in the floor thereof median to that for the rest of the trunk. Having reached the inferior surface of the skull it runs forwards and inwards and dives into a short tunnel just beneath the surface, or more correctly just above the inferior surface. At the anterior end of this little tunnel it turns and runs directly forward close to the inferior surface of the fatty tissue which fills the hollow behind the teeth. In this situation, just above the skin of the roof of the mouth, it breaks up into twigs distributed to the skin on one side of the mid-line.

Immediately the main hyomandibular trunk perforates the floor of the orbit it gives off two branches, one in front and one behind.

The posterior, occipital, branch perforates the cucullaris muscle in three parts to reach the skin behind the orbit; these twigs doubtless supply the sense organs in the canals in that region.

The anterior, which I propose to term the deep internal mandibular branch, drops straight on to the dorsum of the branchial basket and runs forward and anteriorly and laterally, first inside the superior perimysium of the anterior levator of the branchial arches and then under the perichondrium of the pharyngohyal, grooving the cartilage as it crosses it; just here it crosses below the superficial internal mandibular branch. In front of the pharyngohyal cartilage it comes to lie just beneath the skin of the roof of the mouth. In this situation it divides in two and continues forward to the mid-line against the lower jaw below the teeth.

Continuing forward and outward from the foramen in the floor of the orbit the main hyomandibular trunk comes to lie beneath the superior depressor of the lower jaw. It here divides in two, and one of these passes toward the surface between the cartilage and the muscle above the mandibular joint, the other continues forward and laterally behind the cartilage and lower jaw, deep to the muscle.

I propose to designate the latter the superficial internal mandibular branch and the former the external mandibular branch.

The superficial internal mandibular branch is at first placed rather deeply,

but comes to lie between the genio-hyoid and anterior deep inferior constrictor a little lower down. It gives its motor twig to the genio-hyoid muscle as it passes over it and is then continued forward parallel with, but superficial to, the deep internal mandibular branch to the mid-line. It also gives off a branch which is similarly continued forward, but superficial to the genio-hyoid muscle. This latter is essentially a superficial cutaneous nerve, all its twigs turning towards the skin; to reach the skin they perforate the superficial and deep constrictors and may supply motor twigs to those muscles.

The external mandibular branch runs forward, first beneath the anterior fibres of the superior depressor muscle of the lower jaw and then upon the superior protractor of the lower jaw. In front of this last muscle it reaches the internal surface of the large labial cartilage, supplies its motor twig to the inferior protractor of the lower jaw and breaking up intermingles with the mandibular division of the fifth nerve, from which, it will be remembered, it received a communicating twig behind the angle of the mouth. The motor twig to the superior depressor muscle of the jaw is given off as the nerve passes forward under the muscle.

It will be noted that the only branch of the hyomandibular trunk which reaches the skin in the neighbourhood of lateral line organs is that which I have termed the occipital nerve, unless it be that the external mandibular branch sends twigs to the organs in the lower canal near the angle of the mouth. Even so, the occipital nerve hardly seems comparable with Cole's posterior external mandibular lateral line nerve. Our palatine nerves are undoubtedly identical. My deep internal mandibular is apparently his chorda tympani, whilst the two divisions of the main trunk, superficial, internal, and external mandibular seem to represent his post-branchial B and C[1]. Unfortunately Cole's description of the course and situation of these nerves is vague.

The crossed arrangement of the roots of the superficial ophthalmic nerve described by Cole was observed in this form also. The "ventral" root, however, is placed more dorsally than he depicts.

I have depicted the roots and main branches of the fifth and seventh nerves semischematically in text-fig. 4.

The foramen of exit for the vagus nerve is circular at the internal end, but it becomes very markedly antero-posteriorly increased as it penetrates the wall, so that seen in section along that diameter it would be triangular with the apex of the triangle at the inner end.

The vagus divisions separate within the canal, and perforate the cranial perichondrium separately. These issue from the cranium medial to the cucullaris muscle and above the posterior levator of the branchial arches. They turn outward and forward, each having a more forward direction than the one behind. All four branches drop at once on to the dorsum of the branchial basket and split up as described by Cole. The glossopharyngeal nerve is similarly situated in front of vagus root I.

[1] Cole, *l.c.*, p. 651.

I have been unable to see more than the proximal end of the fourth or intestinal root, and of the nervus lineae lateralis I have seen only the end torn off as it issues from the cranium behind the other rami.

The arrangement of the roots of the glossopharyngeal, vagus, and nervus lineae lateralis in *Callorhynchus* is not quite like that described by Cole or figured by Johnston for *Chimaera*.

The four roots of the vagus arise close together from the side of the medulla a little below the mid-line. Of these roots, the first and second are equal in size and are composed of two strands very close together and one above the

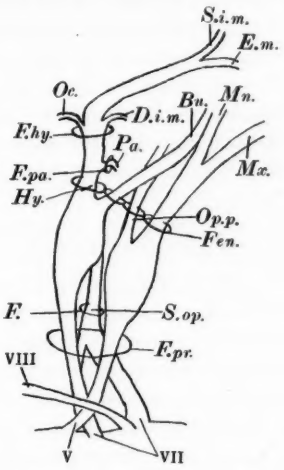


Fig. 4. A semi-schematic presentation of the roots and main divisions and branches of the fifth and seventh nerves. *Bu.* buccal, VII. *D.i.m.* deep internal mandibular ramus of the hyomandibular, VII. *E.m.* external mandibular ramus of the hyomandibular, VII. *Fen.* fenestrated outer end of the foramen prooticum. *F.hy.* foramen hyomandibulare, VII. *F.* foramen ophthalmici, VII. *F.pa.* foramen palatini, VII. *F.pr.* foramen prooticum. *Hy.* Hyomandibular trunk, VII. *Mn.* mandibular, V. *Mx.* maxillary, V. *Oc.* occipital ramus of hyomandibular, VII. *Op.p.* ophthalmicus profundus, V. *Pa.* palatine, VII. *S.i.m.* superficial internal mandibular ramus of the hyomandibular, VII. *S.op.* superficial ophthalmic nerve. VIII, Auditory nerve.

other. The third and fourth one-third larger than the other two are composed of three strands each, placed in line behind one another. These ten strands are all capable of being separated, and the last is so free from the others that it looks almost like a small fifth root. Each of the roots bears its own ganglion, and, though with difficulty, these ganglia may be separated one from the other.

The nervus lineae lateralis arises by a single large root, in which no component strands are recognisable, a little in front of the anterior vagus root, and at a slightly higher level. From this point it passes back and ventrally and comes to lie on the under side of the vagus roots and ganglia in the vagus canal.

The glossopharyngeal root is placed directly below that of the lateralis root, and is quite distinct therefrom, and presents no component fascicules. The nerve passes out and slightly down to the glossopharyngeal foramen.

Of these roots those of the ninth and lateralis lie closest. They are, however, quite separate and placed one below the other, not, as Johnston depicts them, side by side and fused. Cole's description, which is at variance with his illustration, places the roots too close together, for he states that the vagus roots are obscured by the overlying lateralis.

Like Cole I have been unable to find any evidence of lateralis components in the glossopharyngeal nerve. This absence of lateralis components in the glossopharyngeal is interesting. It is later suggested that the Dipnoi, primitive amphibians, may have evolved from forms similar to the Holocephali without the intervention of a teleostome stage.

The absence of the lateralis component of the glossopharyngeal nerve has been observed, so far as I know, only in the Holocephali and the Amphibia; I know of no detailed account of the innervation of the lateral line organs in the Dipnoi.

ARTERIAL SYSTEM

There are the usual five afferent branchial arteries, the anterior two, as in the Elasmobranchs generally, coming off close together. The efferent branchial system is teleostean in type; only the anterior efferent artery is present in each branchial arch. The first, hyobranchial, artery joins the second; their common vessel is next joined by the third. The fourth and fifth unite close to the epi-branchi-cerato-branchial junction, and their common vessel unites with the common vessel of the first three, and the similar vessels from the opposite side, all four together, at the posterior limit of the visceral arches, to form the dorsal aorta.

The hyobranchial efferent artery gives off the mandibular artery seen after it becomes large enough to find. Further dorsally, but before it reaches so high as the top of the epi-branchial, it gives off at the same point two vessels, which I have ventured to designate internal (*seu* posterior) and external (*seu* anterior) carotid arteries. T. J. Parker (1886) described these vessels as arising separately, and found an anastomosis between his anterior carotid and the mandibular. I have been able to dissect ten heads, and in none of them have I been able to find that anastomotic branch. In my dissections I find the mandibular arising from the hyobranchial in much the position Parker depicts his anterior carotid. I have been unable to follow for any distance the tiny vessels which arise from the fine ventral end of the hyobranchial and inter-branchial arteries, and have assumed that they are nutrient vessels for the tissues of the septa.

The internal carotid artery passes directly across to the mid-line where it is joined by its fellow of the opposite side. This anastomosis is so free and accomplished so entirely free from reduction or change in the calibre of the

vessels that it was impossible to determine the limit of each vessel but for the presence of its terminal branch, the cerebral artery, leaving each vessel a little distance on each side of the mid-line. This terminal cerebral vessel passes dorsally through the palatine foramen in the floor of the orbit on its way to that in the sella turcica described above. Before going further one may remark that so free was the anastomosis between the two internal carotid arteries that it was possible in every instance to inject the right and left anterior arterial systems through the common efferent vessel of the hyobranchial and first interbranchial arteries of either side, and in several dissections the fluid was observed passing by this anastomosis.

Inside the cranial cavity the cerebral artery gives off another commissural branch to its fellow of the other side, and one which passes outward and back round the crista sellaris and across the side wall of the cranium to anastomose with that branch of the external carotid which enters the cavity through the prootic foramen (for nerves seven and five). The ophthalmic artery is given off between these two, and it was possible to trace this across the floor of the cranium to the optic foramen.

My injection masses were of necessity very free, and on removing the brain the ruptured ends of the vessels immediately permitted the escape of the mass, so that I lost the continuity of the vessels on to the brain. It would be largely conjectural work, under these circumstances, to attempt the description of those cerebral arteries which retain the injection mass.

I have failed to find any palatine branch of the internal carotid artery.

I have ventured to designate this vessel the internal carotid artery, because it gives off that vessel which perforates the floor of the brain case in the region of the hypophysis cerebri; therein, I believe, presenting a truly homologonomic resemblance to the similarly named vessel in the Amphibia and the Amniota.

On comparing this vessel with the posterior carotid artery of *Mustelis* (T. J. Parker, *loc. cit.*) it will be apparent that it corresponds with that portion of the posterior carotid artery which extends from the hyoidean vessel and the commissure provided by the bifurcation of the anterior continuation of the dorsal aorta, together with the anastomotic trunk which Parker describes as communicating with the anterior carotid of the other side. This latter is of course my terminal branch, the cerebral artery, but in *Callorhynchus* the anastomosis is not crossed but communal. The continuation anteriorly which Parker describes in *Mustelis* is not present in our subject, or at least has not been found. I find a carotid foramen in the floor of the sella turcica of *Carcharhinus brachyurus*, and I conclude that Parker failed to observe in *Mustelis* that the cerebral artery was given off from the cross commissure between the two internal carotid arteries.

The external carotid artery courses upward and slightly backward and perforates the floor of the orbit by way of the hyomandibular foramen. In the orbit it gives off a large branch which passes medially and slightly back-

ward to enter the cranium through the foramen prooticum. Before it traverses this foramen the branch gives off a fairly large twig which passes directly backwards, and, perforating the posterior wall of the orbit, enters the recessus saculi of the auditory capsule immediately below the anterior opening of the anterior vertical canal into that same recess. Within the cranial cavity this "lateral cerebral artery" communicates, as described above, with the cerebral artery. The main vessel after giving off the lateral cerebral and auditory arteries, gives off three to five (the number is thus variable in my dissections), quite small vessels to the contents of the orbit (fat, orbital gland and orbital muscles), and then continues forward to the anterior limit of the orbit. Here it splits up into a number of vessels which are distributed to the structures in front of the orbit. These vessels come off in rapid succession and in some cases amount to an actual dichotomy of the trunk, so that one cannot follow any branch farther and confidently designate it the main trunk.

The mandibular artery courses forward and upward till it comes to lie over the quadrato-mandibular articulation. In this situation it gives off a tolerably large branch which, coursing forward, supplies the tissues of the upper lip. The main branch turns downward, and runs behind the mandible giving branches to the lower lip and jaw.

THE CRANIAL MUSCLES

Muscles innervated by the fifth and seventh nerves

On removing the skin, the lower portion of the head is found to be enclosed in a loose muscular and fascial sheet of tissue, in which three separate muscular entities are recognisable.

1. The *levator operculi* (text-fig. 5, ***L.o.***) arises from the fascia overlying the pectoral (?) muscles. It is, under the skin, the outermost layer of the hinder portion of the wall of the gill cover, and it would appear that its contraction must serve to open the gill slit. Innervated by facial from the external mandibular ramus of the hyomandibular trunk of the facial nerve in its lower part, but also by maxillary of trigeminus above.

2. The *depressor rostri et veli* (text-fig. 5, ***D.v.***) is composed of two sets of fibres. The upper set of fibres arise from the fascial covering of the gills, and is inserted into the upper margin of the velum near its attachment to the cheek. The lower set of fibres are continuous with the anterior fibres of the superficial ventral constrictor, or elevator of the floor of the mouth. They are inserted into the lower free, margin of the velum. Innervated by maxillary division of the trigeminus.

3. The *superficial ventral constrictor* (text-fig. 5, ***S.v.c.***) crosses below the floor of the mouth transversely. The anterior fibres are continuous with the lower fibres of the depressor rostri, and the posterior with the lower fibres of the levator operculi. Innervated by mandibular division of the trigeminus.

These three muscles and the fascia connecting them may be dissected off

the gill cover and the surface of the velum, leaving the deeper portion of the velum, and a deeper layer of fascia over the gill cover, and exposing three deeper muscles.

1. The *anterior deep constrictor* (text-fig. 6, *D.c.a.*) arises from the deep fascia of the velum and passes down behind the angle of the lips and posterior limit of the velum, underneath the anterior end of the depressor rostri et veli. The fibres are nearly parallel with those of the superficial constrictor as they pass from under the other muscle, and soon thereafter become completely parallel and fused with it. Innervated by mandibular division of the fifth nerve, and perhaps also by the external mandibular branch of the hyomandibular of the seventh.

2. The *posterior deep constrictor* (text-fig. 6, *D.c.p.*) arises from a tough mass of fibrous tissue which is attached deeply behind the jaw, and from the

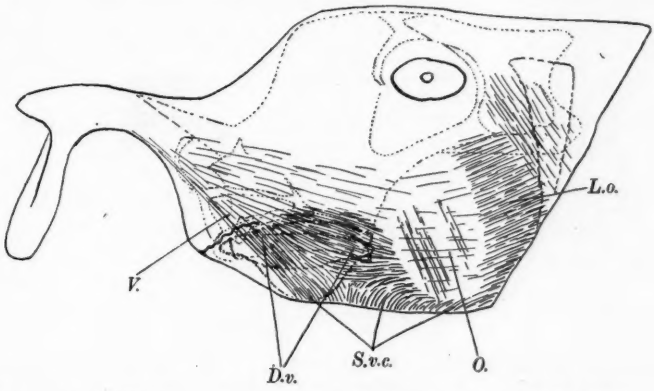


Fig. 5. The most superficial layer of muscles. *D.v.* depressor et tensor veli. *L.o.* levator operculi. *O.* opercular cartilaginous rays. *S.v.c.* superficial ventral constrictor. *V.* velum.

deep fascia over the gill cover. This group of fibres lies directly beneath (deep to) the central portion of the superficial constrictor, and its fibres become intermingled therewith. The whole of the fibres of the ventral constrictors are inserted into a median longitudinal raphe under the lower jaw. Innervated by the mandibular division of the trigeminus nerve, and probably also by the seventh nerve by the superficial internal mandibular ramus of the hyomandibular.

3. The *depressor mandibulae superior* (text-fig. 6, *D.m.s.*) lies beneath, but hast he same origin as the last muscle in its upper portion. It also arises from the lower edge of the upper portion of the suspensorial lamina of the cranium (this portion is shown in text-fig. 6, *D.s.m.*) and its superficial aponeurosis is firmly bound to the edge of that lamina down almost to the lower jaw point. The insertion is threefold, firstly into the inferior edge of the mandible, secondly more deeply into the inner surface of the mandible beneath the

insertion of the coraco-mandibularis and just above the origin of the genio-hyoideus. These fibres are continued along the inner surface of the two cartilages of the lower jaw right to the mid-line, and some are continued right across to the other muscle. Thirdly, the more posterior fibres take a more transverse course, and dipping in under the coraco-mandibularis behind the last set of fibres reach the outer wall of the branchial basket far forward and are attached thereto. Meeting across the mid-line, the two muscles together constitute an intermandibularis. Their action is to depress the lower jaw and slightly elevate the floor of the mouth in front. An interesting tendinous slip from this muscle is continued forward, so that the muscle tends to act as an elevator of the rostrum at the same time that it depresses the jaw. This

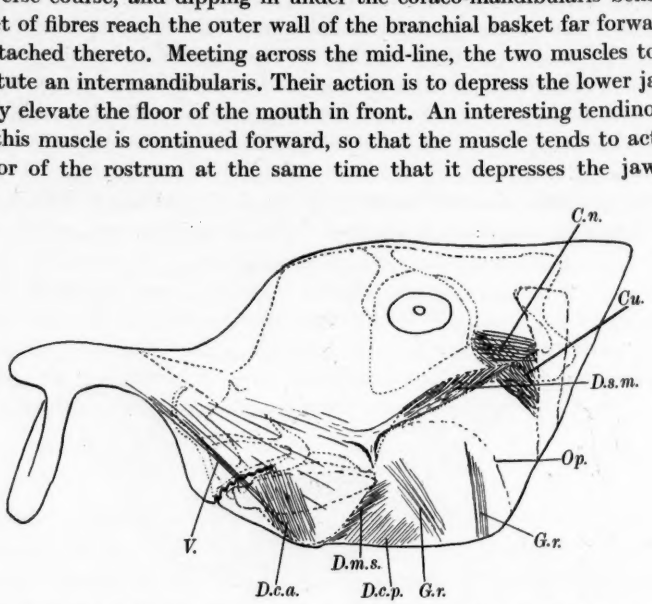


Fig. 6. The second layer of muscles. *C.n.* capiti-nuchal muscles. *Cu.* cucullaris. *D.c.a.* anterior deep ventral constrictor. *D.c.p.* posterior deep ventral constrictor. *D.m.s.* lower fibres of the depressor mandibuli superior. *D.s.m.* depressor mandibuli superior. *G.r.* opercular rays. *Op.* posterior boundary of the opercular fold. *V.* lower edge of the velum.

muscle is innervated by a twig from the hyomandibular division of the facial nerve as it comes forward between the muscle and the cartilage.

When the remainder of the velum and the fascial layer which is continuous with it over the side of the head right up to the sagittal crest is dissected off there comes into view a layer of muscles which operate upon the lips and elevate the rostrum (text-fig. 7). Five muscles are thus exposed and a sixth of the series lies beneath the large inferior labial cartilage.

Before describing these muscles it is necessary to describe briefly the structure of the rostrum. The rostral spine has already been described. It terminates beneath the skin as indicated by the dotted lines in text-figs. 5, 6, and 7. Running forward on either side of it is the strong lateral ligament of the rostrum (text-fig. 7, *L.l.r.*). This arises from the post-nasal spine, and bending sharply forward is attached to the rostral spine. This lateral ligament tapers gradually and is finally lost in the median septum of the rostrum near

the tip. The median septum is a very strong fascial partition which divides the rostrum into right and left halves. The terminal branches of the ophthalmic nerves pass forward on either side of the septum above the lateral ligament; the terminal branches of the maxillary nerves are similarly placed below the ligament. The fibrocartilaginous tip of the anterior upper labial cartilage is placed in the root of the rostrum attached by fibrous connective tissue to the lateral ligament. A thin, but very strong, ligament rises from the sagittal crest immediately above the root of the rostral spine and passing out crosses the lateral ligament at its origin, and then turns down outside, and superficial to the protractor muscle of the upper lip and the anterior upper labial cartilage, and is attached below to the nasal septum just above the margin of the teeth. This I have designated the ligamentum radicis rostri (text-fig. 7, *L.r.r.*).

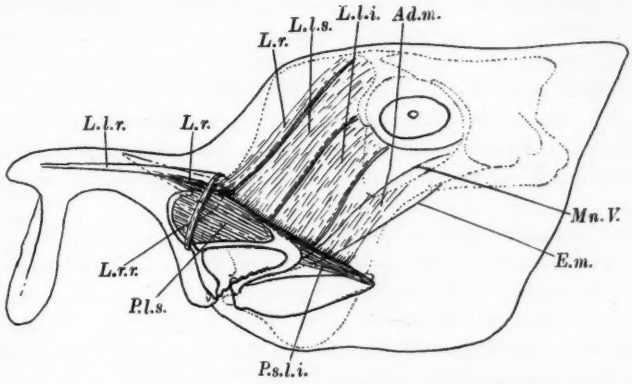


Fig. 7. The third layer of muscles. *Ad.m.* the posterior head of the adductor mandibuli. *E.m.* external mandibular ramus of the hyomandibular trunk of the facial nerve. *L.l.i.* levator labii inferioris. *L.l.r.* lateral ligament of the rostrum. *L.l.s.* levator labii superioris. *L.r.* levator rostri. *L.r.r.* ligamentum radicis rostri. *Mn.V.* mandibular ramus of the trigeminal nerve. *P.l.s.* protractor labii superioris. *P.s.l.i.* protractor superior labii inferioris.

1. The *levator rostri* (text-fig. 7, *L.r.*) arises from the supra-orbital ridge and the sagittal crest just in front of it, and from the deep surface of the fascia which must be removed to expose the muscle. It passes down and forward, turns directly forward under the ligament of the root of the rostrum to be inserted into the lateral ligament of the rostrum. As it passes under the ligamentum radicis rostri it is joined by the upper fibres of the protractor of the upper lip, and with that muscle is also bound to the fibrocartilaginous tip of the anterior upper labial cartilage. Though that impression may not be gathered from the drawing, it was found that the ligamentum radicis was sufficiently loose to permit of the rostrum being elevated by traction on the two levators together. Either acting separately deflected the rostrum to its own side. The motor nerve comes from the maxillary division of the trigeminus, as also do the motor nerves of the other two muscles parallel with this one.

2. The *levator labii superioris* (text-fig. 7, ***L.l.s.***) rises from the supra-orbital crest lateral to the last muscle, and from the fascia over it. Passing down parallel to and behind the levator rostri, it is inserted underneath, deep to, the protractor labii superioris and the labial cartilages into the tissues of the upper lip.

3. The *levator labii inferioris* (text-fig. 7, ***L.l.i.***) arises from the supra-orbital crest behind, and to a slight extent underneath the levator labii superioris, and from the strong periorbital fascial ring. Nearly as broad as the last muscle, its fibres gather to a relatively narrow tendon which passes beneath the posterior upper labial and small lower labial cartilages to gain attachment to the inner aspect of the large lower labial cartilage and tissues of the lower lip just behind the angle of the mouth.

4. The *protractor labii superioris* (text-fig. 7, ***P.l.s.***) arises from the upper margin of the posterior upper labial cartilage and from the spine thereof, and is inserted into the anterior upper labial cartilage above the junction of the two cartilages, and into the flexible fibrocartilaginous tip of the anterior cartilage. It has already been noted that the upper fibres of this muscle join the tendon of the levator rostri. Be it noted that the elevation of the rostrum and its flap would be an advantage when the lips are opened and groping after food.

5. The *protractor superior labii inferioris* (text-fig. 7, ***P.s.l.i.***) arises from the back of the spine of the posterior upper labial cartilage and from the region of the union of that cartilage with the small lower labial cartilage, and is inserted into the perichondrium of the large lower labial cartilage on its outer side close to the posterior end. These last two muscles are innervated by twigs from the mandibular division of the fifth nerve.

6. The *protractor inferior labii inferioris* (text-fig. 8, ***P.***) arises from the outer aspect of the upper margin of Meckel's cartilage near the anterior end and gains attachment to the inner aspect of the posterior one-third of the large lower labial cartilage. The muscle is innervated by the external mandibular branch of the hyomandibular division of the facial nerve.

The *adductor mandibulae* (Masseter of authors) is exposed by the removal of the last six muscles described, together with the labial cartilages. It is a very massive muscle which arises by two heads from the whole of the lateral surface of the cranium in front of the orbit. The anterior head (text-fig. 8, *A*) is much the larger, the posterior (text-fig. 8, *B*) being confined to the quadrate portion of the lateral expansion to which the lower jaw is articulated. Both portions find attachment to the lower jaw per medium of a very strong broad fascial band which is firmly bound to the lateral surface of the jaw, and is continuous below with the broad tendon of the coraco-mandibularis muscle.

This muscle receives motor twigs from both the maxillary and mandibular divisions of the fifth nerve.

The *genio-hyoideus* arises on each side from the fibrous tissue about the

symphysis of the lower jaw. From this origin each muscle passes outward, backward, and slightly down to reach the apex of the angular expansion on the posterior border of the cerato-hyal about the centre of the length of the cartilage. The muscle is ribbon-like, tapering from its tendinous origin to its broader muscular insertion.

I have traced two nerves to this muscle. One a fine twig from the superficial internal mandibular ramus of the hyomandibular trunk of the facial, which reaches the muscle as previously described; the other and larger is a branch of the glossopharyngeal, which is given off from the main trunk of the nerve and is continued forward against the outer aspect of the second and first cerato-branchial cartilages and the cerato-hyal to reach and break up in the mucosa of the side of the mouth, but which gives off a fine twig

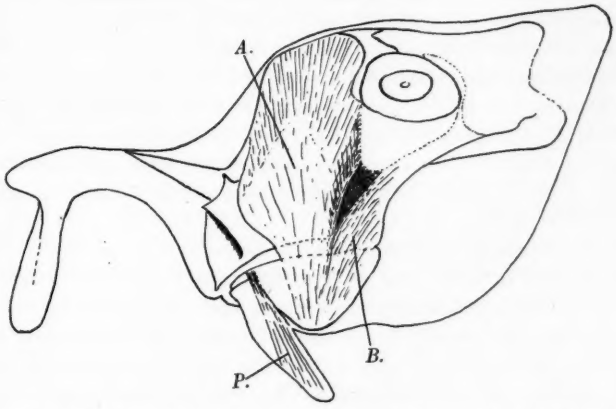


Fig. 8. The adductor mandibulae; anterior head *A*, posterior head *B*. *P*, protractor inferior labii inferioris.

that was traced to the muscle. I believe the former to be the motor nerve, being to some extent persuaded to that view by Cole's statement that in *Chimaera monstrosa* branch *e* of the post-branchial ramus B of the hyomandibular "runs downwards and forwards, *and becomes imbedded in the extensor muscle of the hyoid arch*—i.e. the muscle which draws the arch forwards..." (Cole, 1896, p. 653).

Muscles innervated by the glossopharyngeal and vagus

The *levator arcuum branchialium posterior* arises from the edge of the skull below the posterior orbital wall and just behind it and from a depression on the inferior surface of the skull underneath the hinder and lateral part of the orbit. It has a broad muscular insertion on to the superior surfaces of the second and fused third, fourth, and fifth pharyngo-branchial cartilages. In its course mediad and slightly backward it lies between the inferior surface

of the cranium above and the branchial basket below. This muscle is innervated by a small branch which comes from the main trunk of the second root of the vagus.

The *levator arcuum branchialium anterior* arises from a depression on the inferior surface of the cranium underneath the fore and median portion of the orbit. From this origin it passes laterad and slightly backward to be inserted into the junction of the first and second epi- and cerato-branchial cartilages. The muscle is innervated by a branch from the post-trematic branch of the glossopharyngeal nerve.

The designations of these two muscles are defended later.

I can find no muscle which could be regarded as representing a *subarcualis rectus* (Edgeworth, 1928), but there would appear to be at least one, and it may be four, muscles referable to the transversi ventralis series.

A *sphincter oesophagi* is formed by a fairly broad ribbon of muscle fibres in the wall of the oesophagus immediately at the hinder end of the branchial basket. These fibres are attached above to the fifth pharyngo-branchial, and passing down in the wall of the oesophagus they gain attachment to the elongated fifth basi-branchial and to a median raphe for a short distance behind it. The muscle is innervated by the post-trematic branch of the vagus root three. I have ventured to designate this muscle a sphincter oesophagi for reasons given below.

The other possible representatives of the transversi ventrales series are three long slender muscles, each of which arises from each of the first three basi-branchial cartilages and extends along the outer curve of the cerato-branchial of the same arch. From the origin some of the muscle fibres are "fanned" out into the interbranchial septum in front of the branchial rays. The main bundle, intimately bound to a fine strong tendon which lies against the afferent vessel, is inserted high up on the cerato-branchial cartilage near the insertion of the corresponding external dorsal interarcual muscle.

These may be interbranchial muscles similar to those described by Marion in *Acanthias* and *Raia* (Marion, 1905). On the other hand the very definite main bundle of fibres certainly constitute a transverse muscle capable of acting to open out the three arches they are attached to. They are innervated by the longest post-trematic branch of the glossopharyngeal and vagus roots one and two.

Of *dorsal oblique interarcual muscles* there are three sets, one external and two internal; these latter may be designated medial and lateral internal dorsal oblique muscles.

There are three medial internal dorsal oblique muscles; they arise from the proximal portion of the first, second and third pharyngo-branchial cartilages and are inserted on to the little epi-branchial of the arch behind. To reach this situation they pass above the anterior corner of the pharyngo-branchial cartilage of the arch behind and are inserted on to the dorsal surface of the epi-branchial.

There are four lateral internal dorsal oblique interarcual muscles, and of these the fourth, most posterior, is probably a fused pair. Each arises from the upper end of a cerato-branchial cartilage. The first crosses the ventral surface of the first epi-branchial and is inserted on that piece of the first pharyngo-branchial which extends forward to be attached to the pharyngo-hyal. This resembles the other muscles so closely that although it is attached to components of only one arch I have ventured to regard it as an oblique muscle.

The second and third also cross the ventral surface of their own epi-branchial, but they are inserted on to the pharyngo-branchial cartilage of the arch behind as well as to that of their own arch.

The fourth arises from the cerato-branchials of the fourth and fifth arches and from a membrane between the two and is inserted on to the fused pharyngo-branchial cartilages of the third, fourth and fifth arches.

In all four cases the muscle is broader at its insertion than at its origin, the insertion is muscular, and the area of insertion is quite short and close to the epi- and pharyngo-branchial joint.

All these seven muscles are innervated by post-trematic branches of the vagus and glossopharyngeal nerves.

Three external dorsal oblique muscles are present. Each is a short muscle which arises from the dorsal surface of the epi-branchial of the fourth, third and second arches, and is inserted into the top of the cerato-branchial of the third, second and first arches. They are innervated by post-trematic branches of the glossopharyngeal and roots one and two of the vagus nerve.

The *cucullaris* is apparently represented by a muscle which arises immediately under the skin from the lateral edge of the skull behind the orbit. Tolerably thick and ribbon-like at its origin, it tapers as it passes down, and slightly back, under the fore-edge of the clavicle, to be attached to the anterior border of the supraclavicular cartilage. This in turn is firmly bound, by a continuation of the tendon of the muscle, to the coracoid at about the coraco-clavicular junction and also to the fused pharyngo-branchial cartilages of the last three arches, behind the insertion of the abductor of the posterior portion of the branchial arcade. The cucullaris muscle is therefore an elevator of the pector arch and branchial arcade together.

I have traced four nerves to this muscle. Two of them are twigs from the external mandibular branch of the hyomandibular trunk, which turns backward from the foramen of issue to pass direct to the under side of the cucullaris muscle. Just before reaching the muscle it gives off the two twigs mentioned, and these penetrate the muscle obliquely down, back and out near its surface without giving off discoverable branches. The main branch also penetrates the deep surface of the muscle and ends abruptly without giving off discoverable branches. The three terminals of this nerve had pretty certainly been cut. All my heads had been cut from the body just behind, through or a little in front of the cucullaris muscle. The fourth nerve traced to the muscle

is a fine twig from the trunk of the second vagus root; this divides into several filaments and is doubtless the motor nerve to the muscle. It is probable that the other nerves are lateral line nerves destined to supply organs behind the orbit. The occipital branch of the hyomandibular.

Muscles probably innervated by anterior spinal nerves

My evidence relative to the innervation of the muscles of this group is purely negative. After the most painstaking care in following the branches of the trigemino-facial nerves, and of the glossopharyngeal and vagus nerves, I have been unable to find any twigs of these nerves ending in one of these muscles, or, indeed, terminating so close to one of them as to give rise to a suspicion that, had I been able to follow it further, it might have proven the motor nerve of one of them. A slight reservation should, perhaps, be made here; it is possible that one of the long pre-branchial (post-trematic) branches of the divisions of the vagus and glossopharyngeal nerves may innervate the several branches of the coraco-branchialis. This, however, seems highly improbable; it does not seem reasonable to suppose that branches so fine that I was unable to follow them should be the motor nerves to muscles larger than others whose motor nerves were clearly seen. In none of my specimens of the head of *Callorhynchus* was the proximal portions of the intestinal branch of the vagus and the first spinal nerves preserved. It is assumed that the intestinal branch (root 4) of the vagus has the same distribution as described for *Chimaera* by Cole (1896) and that the muscles of the group are innervated (as in *Squalus*, as described by Norris and Hughes, 1920) by branches from one or more of the anterior spinal nerves.

The *coraco-mandibularis* is brought into view by the removal of the superficial and deep constrictors of the throat. It is a massive roughly pyramid-shaped muscle which occupies much of the space between the lower jaw and the pectoral girdle, below, between and in front of the branchial pouches. It arises from the anterior and lateral surfaces of the coracoid portion of the pectoral arch, and from the deep surface of a strong membranous clothing which invests its inferior surface, and which in turn is firmly attached to the inferior border of the median portion of the arch. One may recognise five portions of the muscle, two paired and one median. The posterior paired portions arise as a single stout bundle of fibres on the ventral surface of the muscle, taking origin in large part from the aponeurotic covering on either side of the mid-line close to the posterior limit of the muscle. They course forward for a short distance only and then turn sharply laterad, in two equal bundles, to become inserted on to the inferior border of the mandible a little in front of the joint, by a strong ribbon of tendinous nature. The anterior paired portions take origin from a broader area below the first pair, and passing more directly forward, but diverging, become attached in similar manner to the inferior border of the mandible in front of the posterior pair. The unpaired portion lies centrally, and deep to the last pair at its origin,

reaching the surface of the muscle as it passes forward to be inserted, similarly to the other portions, into the mandible on either side of the symphasis.

Inasmuch as the fibres of the posterior paired component of this muscle meet in the mid-line whilst still their anterior fibres are almost transverse in direction, they are capable of acting as a posterior deep constrictor of the throat.

The *coraco-hyoideus* is a deeply placed muscle which arises from the superior membranous investment of the coraco-mandibularis, about the mid-line, near the centre of the length of the muscle, and is inserted into the basi-hyal. The muscle is rounded, and tapers all the way from its origin to its fine tendon of insertion. Since its surface of origin is almost in the horizontal plane, the muscle is much longer along its inferior than along its superior surface.

The *coraco-branchialis* is composed of five slips, each of which is easily divisible throughout its length from the others. The muscle arises, without any obvious tendinous assistance, from the anterior face of the coracoid and lower portion of the clavicle. Each slip is inserted by a very short tendon into the junction of hypo- and cerato-branchial cartilages of the five arches. This muscle lies between the branchial pouch and the coraco-mandibularis muscle. The fifth slip has, in addition to the insertion similar to the others, a muscular insertion into the lower half of the outer surface of the fifth cerato-branchial cartilage.

Review of the musculature

The presence of superficial longitudinal muscle fibres over the head is, as far as I can ascertain, a unique feature in the Holocephali. One concludes as one dissects them and finds that they are continuous with transverse fibres ventrally that they are but special modifications of the superficial dorsal constrictors of such a form as *Acanthias* (Marion, 1905). It is further probable that my two deep ventral constrictors are also simply portions of the same muscle layer, more or less dissociated from the more superficial strands by the same force that brought about the changed direction of the dorsal constrictors.

The deep portion of the superior depressor of the mandible is possibly the retractor hyoidei of other elasmobranchs, which has transferred its insertion to the mandible as the hyomandibular cartilage became reduced in size and divorced from the suspensorium. On the other hand it also may be a modified portion of the superficial constrictor. Having in mind the development of these muscles it seems that it is possible that this is the homologue of the anterior intermandibularis, and that the genio-hyoideus is a ventral portion of the same muscle. Compare in this connection the condition in *Polyodon* as described by Edgeworth (1928, p. 25).

The six muscles of the third layer are discussed in more detail later. Suffice it here to state that it would appear probable that they are modifications of the superficial portions of the great adductor mandibularis over which

they lie, and that they are homoplastically paralleled by modifications found amongst the teleostomes, if, indeed, some of them are not actually homologous.

The adductor mandibulae is, of course, completely homologous with the similarly named muscles in other fishes.

It is with some little hesitation that I have designated the two muscles which pass from the dorsum of the branchial basket to the under surface of the skull levatores arcuum branchialium. I cannot, however, find any other muscle with which they may be compared.

Edgeworth (1928, p. 47) has stated that, like the previous muscles, the sphincter oesophagi is one of the muscles that is "absent in all Elasmobranchii." The dicta of this careful investigator may not be lightly disregarded, therefore my designation of this muscle calls for an explanation. Edgeworth (*loc. cit.* pp. 76–8) has described the constrictor oesophagi as developing as a circular investment from the splanchnic mesoblast, whilst the sphincter develops in two halves from the two fifth transversi ventrales which in turn are developed from the fifth branchial muscle plates, except in *Polypterus*, where it is developed from the fourth muscles and plates. In any case the one muscle is developed as a complete circular entity, the other is a paired muscle in origin. Allis (1922, p. 259) describes the transversus ventralis [IV] in *Polypterus* and figures half the muscle. He states that it is continuous behind with the constrictor oesophagi, a muscle which Edgeworth (*loc. cit.* p. 76) states is present in no teleostome. The cogency of these observations is that the description and illustration of Allis applies perfectly to my sphincter oesophagi, except that, in *Callorhynchus*, it is continuous behind with no muscle whatever. There can be no doubt that the muscle in question is a paired muscle, and could not well have been developed as a circular entity.

In one sense this is not a sphincter muscle, because its fibres do not meet above the oesophagus. It is then a matter of choice as to whether it should be designated transversi ventralis V or as I have chosen. Actually it may be said to represent the condition when the two derivatives of the one muscle plate have not yet established their individuality.

Whichever of these names we determine on (implying complete homology with the similarly named muscle in the teleostomes) the little muscle loses none of its interest, for it is present in no other elasmobranch.

Turning next to the dorsal oblique interarcual muscles, Edgeworth (*loc. cit.* p. 63) writes: "The adductores arcuum branchialium are small muscles on the inner side of the branchial bars passing from the epi- to the ceratobranchial cartilages. They are developed in all five branchial segments in the Plagiostomi." My lateral internal dorsal oblique muscles fit this description except that they cross the epi- to reach the pharyngo-branchial cartilages. If we accept them as slightly modified "adductores" then we have only one set of peculiar interarcual muscles to discuss; my external dorsal oblique

present only the peculiarity that they pass from epi- to cerato- instead of from pharyngo- to epi-branchial cartilages.

If we may regard the muscles of my lateral internal set as external, having regard for their insertion on the upper surface of the epi-branchial rather than their origin from the lower surface of the pharyngo-branchial, then they correspond with the lateral dorsal interarcual muscles of the elasmobranchs generally (*vide Acanthias*, Marion, 1905).

Although apparently a smaller muscle the cucullaris of our form compares closely with the trapezius of *Acanthias*, more especially in its insertion than in its origin. I think that there is little doubt that the muscle is correctly designated.

None of the muscles innervated by the hypobranchial (spinal) nerve call for discussion.

Bridge (1904, p. 467) has drawn attention to the many features wherein the Holocephali resemble the teleostomes. He omits from his list the absence of the posterior efferent branchial artery in each arch, although he recorded it on an earlier page (p. 333).

Callorhynchus in its complicated lip skeleton and musculature presents another feature which belongs to this category. True, our subject presents these features in a more advanced condition than some, if not all, of the other recent Holocephali. They are little less significant to the student of evolution on that account, because there is a range of variation in the development of these structures, no less wide, amongst the members of the teleostomi. With a view to a better comprehension of the significance of the structures in *Callorhynchus* it is proposed briefly to pass in review some of the variants in the teleostomes.

It would appear that the various muscles of the fish head innervated by the fifth nerve are not subject to homologisation by considerations of their points of origin; and though, in their insertions and functions, the muscles present a much greater constancy, the attempt, which follows, to homologise them on this evidence must be regarded as presenting only the probabilities.

Just how many variants are presented by the teleostomes it is not yet possible to say. The following muscles, however, appear to be tolerably constant, and may be regarded as standard for the whole group:

(1) A small muscle which so acts upon the maxillary labial as to draw that bone back and up into the cheek, and more or less under the lachrymal bone. This, I have ventured to designate the adductor labii superioris.

(2) A superficial portion of the adductor mandibulae, which, though connected to the tendon of the deeper portion, acts to retract and elevate the angle of the mouth. This by reason of its insertion into a very strong (and constantly present) band of ligament which is attached above to the distal ends of the maxillary and premaxillary labial bones, and below into the coronoid process of the lower jaw (here termed the retractor anguli oris).

(3) The adductor mandibulae superior.

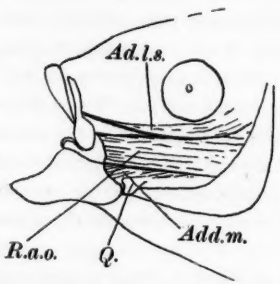
(4) The adductor mandibulae inferior.

I have not been able to consult Vetter's classical works, but they have been so extensively quoted by later workers that one is able to state quite confidently that my adductor labii superioris and retractor anguli oris are portions of Vetter's adductor mandibulae 1, my adductor mandibulae superioris comprises his add.m. 2 and 3, whilst my add.m. inferioris is his add.m.ω (= ad.m. 4 of Adams, 1919).

So far as my investigation enables me to judge, the features of the adductor mandibulae inferioris are so constant that the description of the muscle in *Scomber* or *Amia* given so thoroughly by Allis (1903, 1897) would apply in all essential points to the muscle in every case where it is present. That being so it were a waste of time on my part to describe it in any form.

On the other hand the other three muscles vary within fairly wide limits, and the following notes and sketches are offered.

Girella cuspidator (text-fig. 9). The adductor labii superioris arises from the upper end of the preoperculum, runs horizontally forward below the floor



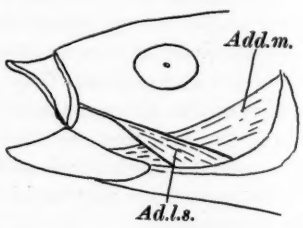


Fig. 9. *Girella cuspidator*. *Add.m.* adductor mandibulae. *Ad.l.s.* adductor labii superioris. *Q.* quadrate bone. *R.a.o.* retractor anguli oris.

Fig. 10. *Mugil cephalus*. Lettering as in fig. 9.

of the orbit, under cover of the subocular scutes and lachrymal bone, and is inserted into the middle of the length of the maxillary labial bone. In its superficial portion this muscle is on the same level as the retractor anguli oris, and its deeper portion beneath the orbit lies against the upper fibres of the adductor mandibulae superioris. The retractor anguli oris takes origin from the lower half of the edge of the submerged area of the preoperculum, and, running horizontally forward, it is inserted into the strong fibrous fascia at the angle of the mouth. Its tendon is attached, deeply, to that of the adductor mandibulae superioris.

The adductor mandibulae superioris arises from the whole of the submerged area of the preoperculum, and from the outer aspect of the metapterygoid. It is inserted into the coronoid process and into the tendon of the adductor mandibulae inferioris. Deeper and more superficial portions corresponding to Vetter's add.m. 2 and 3 are readily recognisable.

Mugil cephalus (text-fig. 10). The adductor labii superioris arises low

down, on the horizontal edge of the submerged portion of the preoperculum. From its origin it passes up and forward to be inserted by a fine, but thoroughly strong, tendon into the back of the maxillary labial bone at the junction of the middle and outer thirds of its length. The muscle lies entirely superficial to the adductor mandibulae superioris.

The retractor anguli oris is not developed as a separate entity, but is completely blended with the adductor mandibulae superioris. The compound muscle arises from the outer surface of the posterior components of the quadrato-palatine arch. It is inserted into the fascia of the angle of the mouth, the coronoid process and the tendon of the adductor mandibulae inferioris. In this species I have been unable to find any definition of the muscle into portions which could be regarded as equivalent to Vetter's components of the add.m. except the add.m.ω.

These two forms may be said to present variations of the arrangement of these muscles which is to be regarded as typical of the acanthopterygian Fishes as a class.

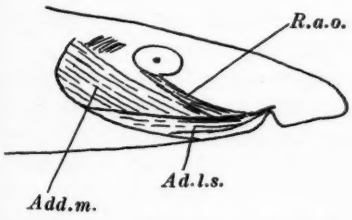


Fig. 11. *Gonorhynchus Greyi*. Lettering as in fig. 9.

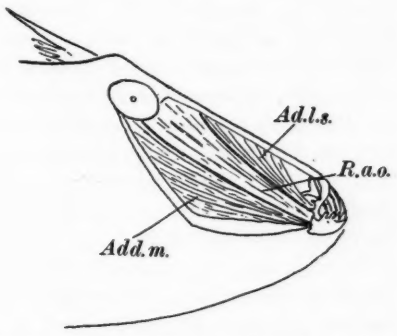


Fig. 12. *Balistapus aculeatus*. Lettering as in fig. 9.

Gonorhynchus Greyi (text-fig. 11). The muscles of the group are all, in my specimens, inseparably fused at their origin. The lower fibres are continued forward, above the mouth, in the velum, and by the fibres of this structure gain insertion into the side of the pre-ethmoid bone under the lachrymal. As the velum is firmly bound to the maxillary labial as it crosses it, this muscle acts both as a tensor veli and as an adductor labii superioris. The upper fibres of the adductor mandibuli superioris are gathered on to a tendon which is inserted into the fascia of the angle of the mouth. Some of this last bundle of fibres join the tensor veli muscle. The adductor mandibulae superioris takes origin from the hinder components of the quadrate-palatine arch between the divergent bundles of the other two muscles. The insertion is into the upper edge of the lower jaw in front of the joint. The adductor mandibulae inferioris is reduced to a mere remnant.

Balistapus aculeatus (text-fig. 12) resembles *Girella* in the general arrange-

ment of the muscles, but with the difference that all of them arise in front of the orbit. Herein this group of Fishes resemble the Holocephali. I know of no other forms in which the whole of the muscles of the face and of mastication are situated entirely in front of the orbit.

The adductor labii superioris arises from the under side of the lamina of the prefrontal (text-fig. 12) and is inserted into the spur on the back of the maxillary labial.

The retractor anguli oris arises from the descending portion of the prefrontal, and, passing down and forward beneath the lower end of the premaxillary labial, is inserted into the short strong fibrous band which joins that bone to the coronoid process of the mandible.

The adductor mandibulae arises from the covered area of the preoperculum, from the hyomandibular bone and from the floor of the orbit and is inserted into the inner aspect of the mandible, in front of and above the joint.

There is no adductor mandibulae inferioris.

Hemirhamphus intermedius. In this form there is present only the adductor mandibulae superioris. This arises from the outer aspect of the hyomandibular and preoperculum, and is inserted by a strong tendon into the upper edge of the mandible just in front of and above the joint, and into the fascia anguli oris. No one of the other muscles of the group is present.

Fistularia petimba. Here also only the adductor mandibulae superioris is present. This arises from the front wall of the orbit and from the roof, floor, and inner wall of the sulcus formed by the union of the hyomandibular and prefrontal bones. The area of origin does not extend far forward of the orbit. In front of the muscle its long tendon extends forward along the sulcus, and is inserted into the coronoid process, well in front of the joint. Just before reaching this point it passes inside the raphe joining the upper and lower jaws and is attached thereto.

Anguilla reinherdti. There is no trace of the retractor anguli oris or of the adductor labii superioris. This is, of course, associated with and due to the fact that there are in the Apodes no labial bones and no complicated lip folded upon itself when the mouth is closed and drawn down to make a side screen to the mouth when open. In short there is no labial bone to be adducted and no secondary anguli oris to be retracted.

The adductor mandibulae superioris is a very massive muscle; its wide area of origin includes (1) the posterior fascial wall of the orbit; (2) a median sagittal intermuscular septum (between the muscles of either side) which extends from the posterior boundary of the orbit to the hinder limit of the skull; (3) the dorsum of the skull lateral to this septum; (4) the dorsal surface of the post-frontal; (5) a small area on the anterior face of the quadrate; (6) the deep anterior surface of the preoperculum; (7) a fibrous septum between it and the muscles behind it. It is inserted by a very stout tendon into the coronoid process, and into a deep pit on the inner side of the bone. Tracing this tendon back again, it is found to expand fanwise, or rather into

an open brush. The fibres of this brush extend a long way back into the mass of the muscle. Anteriorly the fan-like expansion becomes intimately associated with the strong fibrous strengthening of the angle of the lips, and posteriorly a strong band finds attachment to the outer edge of the quadrate at a little distance above the articular surface. This last slip doubtless acts as a check ligament, limiting the extent of the gape.

There is no adductor mandibulae inferioris.

It may be pointed out now that these modifications affect muscles which are undoubtedly derivatives of the main adductor mass of the lower jaw.

Reviewing the complicated musculature and skeletal support of the lips and lower jaw of *Callorhynchus*, one may be permitted to offer the suggestion that they present us with a complicated attempt to carry out the general design perfected in the teleostomes, the skeletal support an imperfect forecast of the superior labial bones (heretofore, except by the writer, termed maxilla and premaxilla), the musculature containing a more perfect forerunner of the retractor labii superioris and retractor anguli oris so constantly present in the teleostomes.

If we now briefly survey the foregoing description of the musculature of the head of *Callorhynchus* the outstanding features of importance will be found to be: (1) the presence of three of those four muscles which Edgeworth pointed out were absent in all elasmobranchii, viz. levatores arcuum branchialium, transversus ventralis, and sphincter oesophagi; (2) the presence of a complicated musculature activating the lips and lower jaw, which seems to foreshadow the more simple arrangement found in the teleostomes.

CONCLUSION

It may be said of the extinct forms of animal life preserved to us in the palaeontological record, that were we able to interpret them aright, we should divide them into those which had proven failures and those which had been successes in Nature's try-outs along the courses of evolution. The successes, of course, arranged in their proper sequence would present us with a more or less complete genealogical tree for the existing forms. The failures in their turn properly arranged as branches of this tree (whose single tap-root is buried deep in past ages) would appear as abruptly broken branches, attached nearer or further from the root.

If Nature's objective was the evolution of the human species, then she was entirely successful only with the growth of that branch which produced as its ripened fruit Man. This, however, were a foolish conceit. Nature was successful so long as she maintained plastic, and capable of further modification, each and every branch. She was, in fact, successful with every one of the branches whose fruit may be recognised in the various classes of the living animals.

But each and every one of these branches bore broken branchlets and twigs; the fossils are their record. Some of these broken branchlets bore many

twigs, and some of these twigs were able to adapt themselves to the changing conditions as successive geological ages passed. We call them "persistent types." Perhaps the most remarkable of these persistent types is the brachiopod *Lingula*, which comes to us practically unchanged from Cambrian times. Among the Vertebrata one may mention all three of the Dipnoi and all the living members of that heterogeneous group of Fishes which we know as the ganoids. The Holocephali also fall among the number.

There is, however, another and more valuable way of regarding these persistent types. They may be looked upon as unsuccessful essays in evolution, as variants of the successful forms in the centre of the full current of evolution.

Regarded thus the Holocephali become much more significant and interesting to the student of evolution. If this concept be a correct one, then they will be regarded as presenting us many of the features which Nature early imported into the elasmobranch stock, in her efforts to evolve the bony Fishes. Perhaps they also present us with some resemblance to the early condition from which the Dipnoi and the Amphibia derive their solidly anchored suspensorium of the lower jaw.

The complex skeletal and muscular apparatus for the movement of the lips may be regarded as having failed, because the skeleton of the upper lip neglected to develop the teeth that were the secret of the success of the bony Fishes nearer the centre of the evolutionary stream of the Fishes. Deep down beneath this failure, however, was the germ of another line of evolution. Hidden underneath the futile lip mechanism was the solid hinge of a powerful lower jaw, and a compact and adequate adductor musculature attached to the skull itself, not to the suspensorium of the jaw. These are features which are reproduced with remarkable faithfulness in the Dipnoi.

In recent papers on the Evolution of the Anamniota (1931) I maintained that the Chondrostei were more correctly regarded as bony elasmobranchs than as members of the bony-fish family. I further pointed out that a natural corollary of this was that the elasmobranchs and bony fishes came from a common stock. The Holocephali present us, as it were, the converse of this same proposition. They are undoubted elasmobranchs which present some of the teleostean features possessed by individual members of that unstable menstruum from which were ultimately crystallised out the elasmobranchs, as a first successfully established homomorphic group.

Consideration of the fixed lower jaw joint and its compact musculature, on the other hand, gives rise to legitimate doubt as to whether it may not have been that already that unstable menstruum did at the same time contain the evolutionary potential which was capable of producing both the dipnoan and ganoid stock side by side.

The geological antiquity of the various groups does not contraindicate such a possibility.

In addition to the list of features given by Bridge, wherein the Holocephali

approach the teleostomes and depart from the elasmobranchii, attention may be drawn to the large lateral internal cranial fenestra and the absence of the posterior efferent branchial arteries. To these the present work adds the levatores arcuum branchialium, transversus ventralis V and the sphincter oesophagi muscles.

In most of these features the Holocephali resemble also the Dipnoi, and one may add here the firmly ankylosed lower jaw suspension and the absence of lateralis components in the make-up of the glossopharyngeal nerve.

For the material whereon the present study is based I have to thank Dr J. Allan Thomson, Director of the Dominion Museum, Wellington, New Zealand, who obtained a very fine series of heads for me through the Hon. G. M. Thomson, from the Portobello Fish Hatcheries at Otago Harbour.

I have to record my grateful thanks to the Australian Council for Scientific and Industrial Research for their assistance by a grant which has helped to make this work possible, and to my daughter Miss Betsy Leighton Kesteven for the two drawings on Plate I.

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EXPLANATION OF PLATES

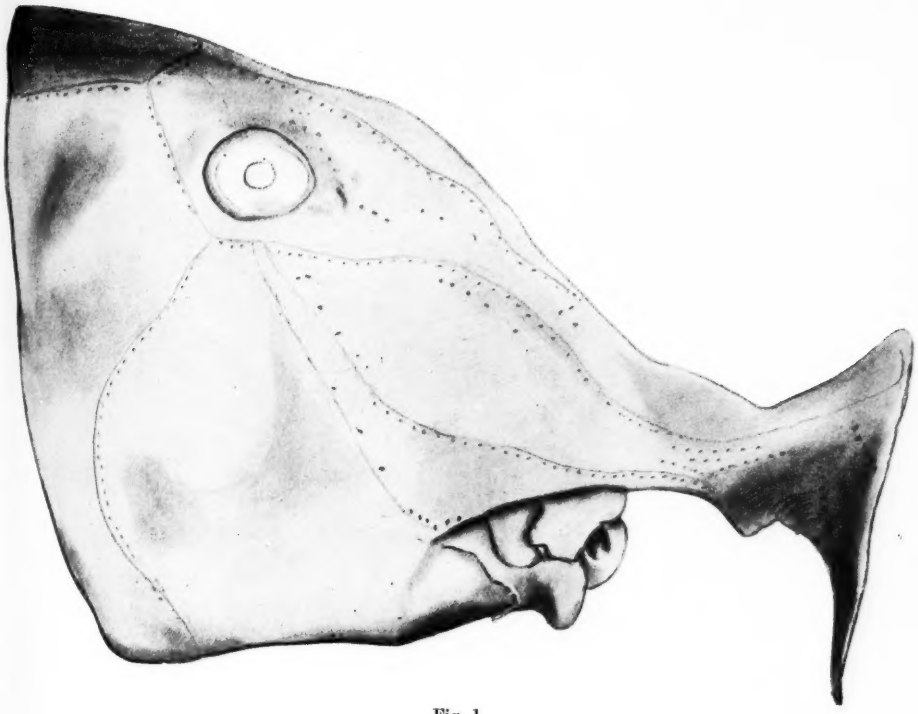
Plate I

Figs. 1 and 2. Side view of the head and front view of the mouth and nasal aperture.

Plate II

Fig. 3. Side view of the skull. *A.c.* anterior superior labial cartilage. *L.i.c.* large inferior labial cartilage. *M.c.* median nasal cartilage. *P.c.* posterior superior labial cartilage. *R.l.* root of the lateral ligament of the rostrum. *S.c.* superior anchoring labial cartilage. *S.i.c.* small inferior labial cartilage. IX and X, nerve foramina.

Fig. 4. Skull cut open along the median sagittal plane, seen from within. *D.e.* canal for the ductus endolymphaticus. *I.c.* inferior, anchoring labial cartilage. *Oph.VII.* foramen for superficial ophthalmic division of facial nerve. *Oph.c.* posterior aperture of the ophthalmic canal. *Oph.V.* foramen of entry of the ophthalmicus profundus. *O.l.* otic labyrinth. *Pi.* pineal recess. *Pt.* subpituitary fossa. *S.t.* sella turcica. II, III, IV, V, VI, VII, IX and X, nerve foramina.



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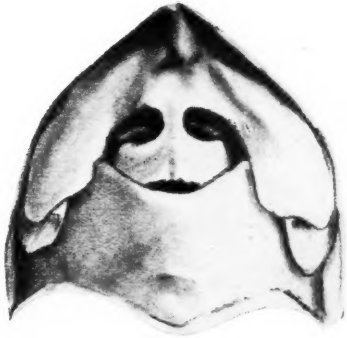
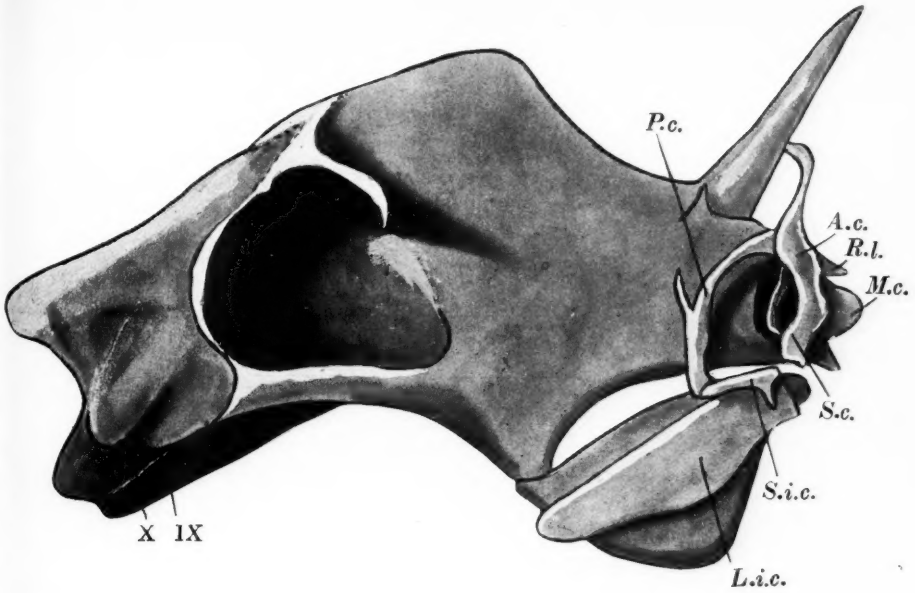


Fig. 2.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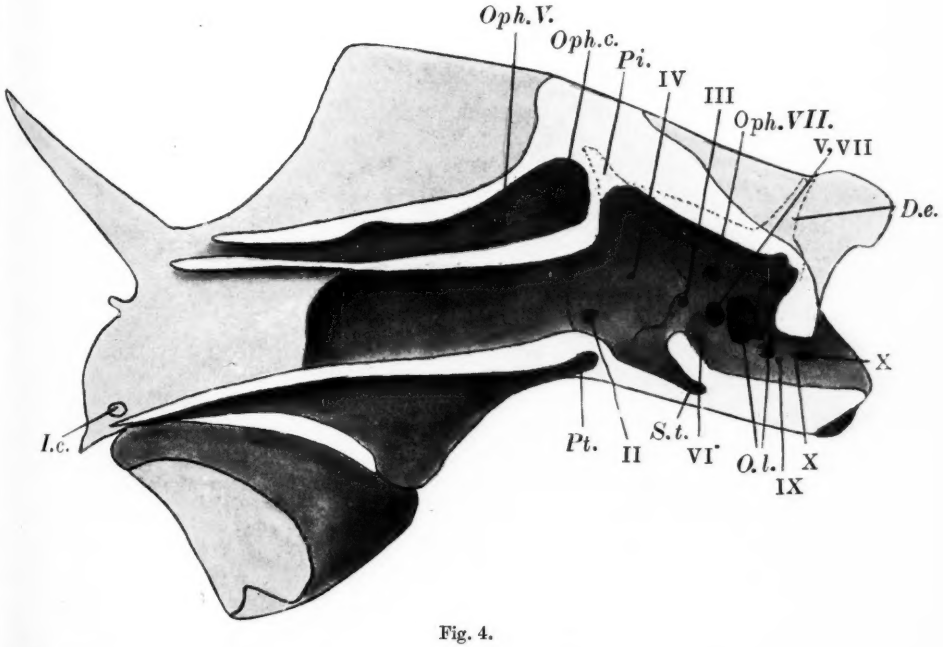
X
IX

Fig. 3.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O.l.
X
IX

Fig. 4.

NOTES ON SOME ANOMALOUS GIBBON SKULLS[1]

By A. TINDELL HOPWOOD, M.Sc., F.L.S.

All the material described forms part of the collections in the Department of Zoology of the British Museum. For the opportunity of studying it I am indebted to the kindness of Dr W. T. Calman, F.R.S., Keeper of the Department, to whom I tender my best thanks for the facilities accorded to me.

Most of the skulls are of immature animals, but three are fully adult or nearly so. Since very little appears to be known of the changes which take place in the skulls of gibbons during life, the age of each specimen is expressed in terms of the eruption of the teeth. The Register Numbers are those of the Department of Zoology, and the specific names employed are those under which the skulls are classified in the Department.

Hylobates leuciscus (Schreber)

Three skulls of this species show a well-marked fronto-temporal articulation; they are registered 5b, 9.1.5.2, and 9.1.5.3. That showing most anomalies is described first.

9.1.5.2. A young female with the deciduous premolars and first molar fully erupted on either side; the second molars are still in their crypts. There is marked asymmetry of the brain case. The left parietal is the more arched and inflated; the highest point of the skull is to the left of the sagittal suture.

The crista occipitalis externa passes slightly to the left, and after 11 mm. is lost in a large boss, which is separated from its smaller fellow on the right by a wide, shallow groove. The left squama occipitalis has a deep notch which accommodates two sides of a fonticular bone in the position of the mastoid fontanelle.

The arms of the basilar part of the occipital, which terminate in the condyles, are asymmetrical. The left is 6 mm. wide; it passes outwards more rapidly than the right, which is 4 mm. wide.

The left parietal is larger than the right; the respective lengths of the inferior margins are 34·5 and 31·7 mm. Each bone articulates with its fellow, as well as with the temporal, occipital, and frontal. Owing to the interpolation of a large process from the frontal (fig. 2) neither articulates with the great wing of the sphenoid.

The frontal suture is still open. The left frontal is rounder and more inflated than the right, and its nasal part is much wider; consequently the frontal suture in its lower portion is displaced to the right. The left nasal part articulates with both nasal bones, and with the frontal process of the right maxilla; hence the

[1] Published by permission of the Trustees of the British Museum.

right frontal does not articulate with the right nasal (fig. 6). Each frontal bears a large process, 9·5 × 14 mm., at its inferior angle. These processes articulate with the temporal, parietal, zygomatic, and sphenoid. Thus the pterions show a fronto-temporal articulation instead of the more usual spheno-parietal one.

There are four large fonticular bones (fig. 3). The largest is kite-shaped. It fills the frontal fontanelle; greatest length 28 mm., greatest width 10 mm. Two others are in the occipital fontanelle; the left (10 × 8 mm.) is larger than the right (9 × 4·5 mm.). The fourth, previously mentioned as being bounded by the occipital on two sides, is in the left mastoid fontanelle; it measures 11 × 7 mm.

9.1.5.3. A young female from the same locality as the preceding. The milk teeth are all in use, but the first and second molars are still in their crypts. This skull appears to be younger than 9.1.5.2.

The frontal suture is closed, as well as part of the coronal suture. The arrangement of the sutures on the roof of the skull is shown in the figure (fig. 9). Both pterions have a fronto-temporal articulation best seen on the left (fig. 4); the right side is damaged. The left wing of the sphenoid is very narrow; its frontal margin is 1 mm. wide.

The nasal region is peculiar, but its structure is obscured by three large cracks. The nasal bones, which were very small, and which have been lost in maceration, were excluded from contact with the frontals by an articulation of the frontal processes of the maxillae for 12 mm.

5b. A young adult of unknown sex; second molars erupted, third molars still in the crypts.

Both pterions have a fronto-temporal articulation (fig. 1). There is a small triangular bone in the frontal fontanelle. Its frontal margin is 9·5 mm. long, whereas the parietal margins are 7·7 mm. long.

Hylobates leucogenys, Ogilby

26.10.4.3. A young male. Deciduous dentition fully erupted; first and second molars still in their crypts.

The main interest in this specimen is its unusual development of sutural and fonticular bones. There are five large bones in the coronal suture which entirely exclude the frontal from articulation with the parietals except for a distance of 4–5 mm. in the left, and 12 mm. in the right temporal regions. Three bones are on the left, and two on the right, of the sagittal suture. The occipital fontanelle is occupied by six irregular bones with complex dentate sutures (fig. 12). Two bones are to the left, and four to the right, of the sagittal suture. The pterion has a spheno-parietal articulation (fig. 11).

Hylobates hainanus, Thomas

11.2.24.4. An adult male with the third molar fully erupted.

This specimen shows a well-marked zygomatic-parietal articulation on either side of the skull (fig. 5). There is one sutural bone between the right

mastoid and the occipital. The specimen differs from all the other specimens of *Hylobates* skulls mentioned, except 5b, in having small, but definite, mastoid foramina.

Hylobates sp.

15.12.1.1. A sub-adult male with the second molar in wear, and the third still in the crypt.

Both pterions show a pronounced zygomatic-parietal articulation (fig. 7).

Symphalangus (= *Siamanga*) *syndactylus* (Raffles)

84.4.24.8. A young skull, sex unknown, with the full deciduous dentition in use, and the first and second molars still in their crypts.

The left pterion shows a narrow, 3 mm., zygomatic-parietal articulation. There is a similar narrower, 1·5 mm., articulation in the right pterion (fig. 8). At the lambda there is a small anomalous bone 5 mm. in diameter. The mastoid foramina are larger than in any other gibbon's skull examined; diameter of the left foramen 3 mm., of the right 1·5 mm.

19.11.12.2. An adult female with the third molars fully erupted. All the cranial sutures are still open.

Both pterions have a zygomatic-parietal articulation (fig. 10). There is a triangular bone in the posterior part of the frontal fontanelle; its anterior side is 8 mm. long; the left and right sides measure 10 and 11 mm. respectively. Another bone, at the lambda, measures 7 × 4·5 mm., and a third bone, 5 mm. to the left, is 2·5 mm. in greatest diameter.

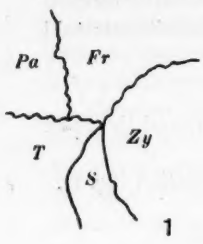
The chief interest in this skull is the presence of a fourth molar, still in the crypt, on either side of the palate. Both teeth are impacted, and have displaced the third molars inwards, causing a posterior narrowing of the dental arch. The occlusal surface of the left tooth faces downwards, outwards, and backwards. That of the right tooth faces downwards and inwards. The mandible has the normal three molars on each side.

REMARKS

Earlier observers (Anoutchine, 1878; Ranke, 1898) found that among the pterions of gibbons a spheno-parietal articulation was the general rule, and that not more than 13 per cent. of the cases had a fronto-temporal articulation. Collins (1925) has raised this figure to just over 40 per cent., but the percentage in the British Museum collection is not nearly so high.

Collins only records one skull of *Hylobates*, species not stated, in which the parietal articulates with the zygomatic. As he points out, this is the predominant condition among the Cebidae. He does not record this articulation in *Symphalangus*.

Fourth molars are of extreme rarity among the Hylobatidae. Remane (1921) describes one case of fourth upper molars in *H. leuciscus*, and quotes an



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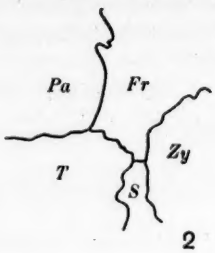

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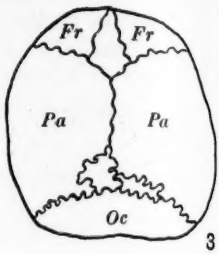

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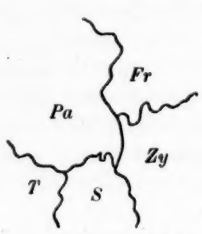

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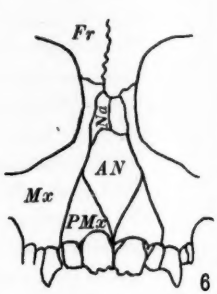

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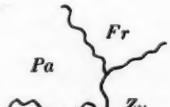

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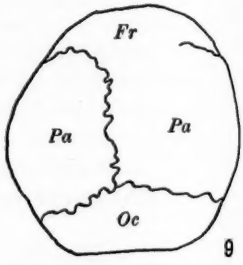

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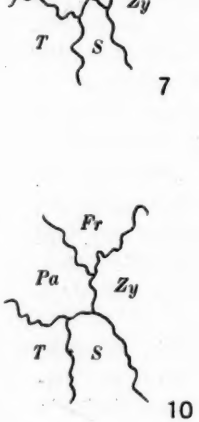

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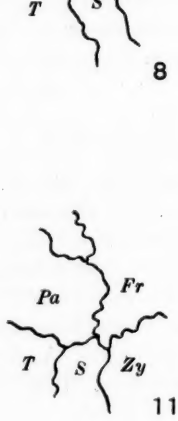

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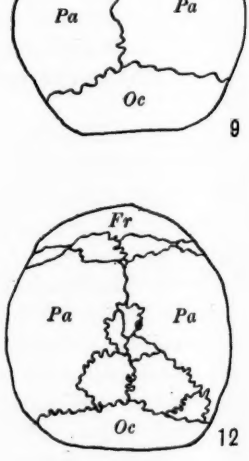

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Figs. 1–12.

old record (Giebel, 1855) of fourth lower molars in *Symphalangus*. Duckworth (1915) says that supernumerary molars are "very infrequent" among the Hylobatidae, and that none was found in an examination of fifty-one gibbons' skulls.

SUMMARY

The form of the pterion in eight gibbons' skulls is recorded; four have the parietal in contact with the zygomatic, three have a fronto-temporal articulation, and the last has a spheno-parietal articulation. Their sutural and fonticular bones are described, as well as two cases of abnormal articulation of the nasal bones.

A skull of *Symphalangus* has a fourth molar in each maxilla.

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EXPLANATION OF FIGURES

Fig. 1. *Hylobates leuciscus*, regd. 5b. Right pterion showing fronto-temporal articulation, and form of the upper portion of the ala magna. Enlarged.
Fig. 2. *H. leuciscus*, regd. 9.1.5.2. Right pterion showing fronto-temporal articulation. Enlarged.
Fig. 3. *H. leuciscus*, regd. 9.1.5.2. Skull cap, viewed obliquely from behind, showing anomalous bones in the frontal and occipital fontanelles. Reduced.
Fig. 4. *H. leuciscus*, regd. 9.1.5.3. Left pterion, reversed for comparison with the other diagrams, showing fronto-temporal articulation. Enlarged.
Fig. 5. *H. hainanus*, regd. 11.2.24.4. Right pterion showing a zygomatic-parietal articulation: Enlarged.
Fig. 6. *H. leuciscus*, regd. 9.1.5.2. Part of face showing the relationships of the nasal bones. Enlarged.
Fig. 7. *Hylobates* sp., regd. 15.12.1.1. Right pterion showing a zygomatic-parietal articulation. Enlarged.
Fig. 8. *Symphalangus syndactylus*, regd. 84.4.24.8. Right pterion. The parietal just meets the zygomatic. Enlarged.
Fig. 9. *Hylobates leuciscus*, regd. 9.1.5.3. Skull cap, viewed obliquely from behind, showing the irregular closure of the sutures. Reduced.
Fig. 10. *Symphalangus syndactylus*, regd. 19.11.12.2. Right pterion showing zygomatic-parietal articulation. Enlarged.
Fig. 11. *Hylobates leucogenys*, regd. 26.10.4.3. Right pterion showing the normal spheno-parietal articulation. Enlarged.
Fig. 12. *H. leucogenys*, regd. 26.10.4.3. Skull cap viewed obliquely from the rear, showing the anomalous bones in the coronal suture, and occipital fontanelle. Reduced.

The following contractions are used in the figures: *AN*, anterior nares; *Fr*, frontal; *Mx*, maxilla; *Na*, nasal; *Oc*, occipital; *Pa*, parietal; *PMx*, premaxilla; *T*, temporal; *S*, sphenoid; *Zy*, zygomatic. Sutural and fonticular bones are not lettered.

ANATOMICAL NOTE

A NOTE ON THE ORIGIN OF THE M. SCALENUS MEDIUS

By A. J. E. CAVE

Anatomy Department, University of Leeds

Textbooks still manifest some diversity of opinion concerning the cervical attachments of the middle scalene muscle, the several accounts differing as to both the precise site of origin of the constituent muscular slips and their actual number. Without space-consuming quotation, it may fairly be stated that almost all authorities regard the atlantal slip as an additional variation, whilst most favour the posterior tubercles of the cervical transverse processes as the detailed origin of fasciculi, although Bryce in Quain (7) correctly agrees with Eisler, Poirier and Le Double in giving the costo-transverse lamella.

Recent enquiry upon anatomical and autopsy material offered some explanation of the textbook discrepancies, which reflect the variability of the scalene musculature as a whole, and the difficulty frequently encountered in determining accurately the limits of a given member of the group, a difficulty notably affecting the medius, whose axial and atlantal slips of origin are often complicated by the presence of anomalous muscle bundles (Mm. intertransversarii longi, recti laterales longi, etc.) and by the variations of the anterior intertransverse muscles of the atlanto-axial and succeeding segments.

Examination of sixty subjects, of either sex and varying in age from infants to aged adults yielded the following results:

(*a*) *Vertebral numerical origin of Sc. medius*

From Cerv. vert.	1	to	7	inclusive in	37	subjects (61 %)
„ „	2	to	7	„	9	„ (15 %)
„ „	3	to	7	„	6	„ (10 %)
„ „	3	to	6	„	6	„ (10 %)

(In two cases no exact definition was possible.)

It is thus apparent that an atlantal slip, which might well be regarded as typical of the "ideal" muscle, occurs in the great majority of instances, whilst in only 20 per cent. or so of cases is an axial slip wanting; these slips are dealt with in detail below regarding attachment and relations.

(*b*) *Precise vertebral origin*

In the lower five cervical vertebrae, the individual medius slips invariably took origin from the lateral edge of the intertubercular (= costo-transverse) lamella, commonly extending dorsally to become continuous with the origin of the posticus from the posterior tubercles, and occasionally continuous ventrally with the origin of anticus when that muscle encroached upon the lamella, as is sometimes its habit. (Scalenus anticus, commonly confined to the fourth, fifth and sixth transverse processes and never arising higher than from the third, shares the anterior tubercle with the M. longus colli and the M. rectus capitis anticus major. The precise extent of its tubercular attachment varies reciprocally with the degree of development of these muscles; thus when longus colli is well developed the anticus occupies the summit of the anterior tubercle and may extend therefrom on to the intertubercular

lamella; when the rectus capitis is exuberant, the anticus is forced on to the postero-lateral aspect of the tubercle, where the two muscles may exhibit continuity of attachments.) Despite their blending at origin, the middle and posterior scalenes are usually thereafter clearly distinct.

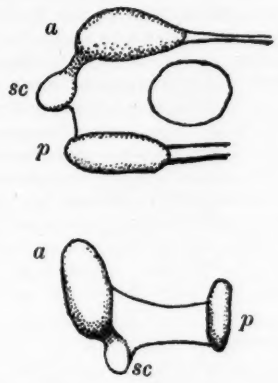

Fig. 1. Superior and lateral views of cervical transverse process to show anterior (*a*), posterior (*p*), and scalene (*sc.*) tubercles.

(*c*) *The cervical scalene tubercle*

The scalenus medius appears to be responsible for the not infrequent occurrence of the cervical scalene tubercle, the "tubercle moyen ou scalénique" first described by Juvara and Dide (4) and regarded by Le Double (5) as, "rien autre chose que la partie inférieur du tubercule antérieur," as, indeed, it is. (See fig. 1.) The French authors believe this tubercle to be produced by scalenus anticus, but from its situation (when present) on the third and fourth vertebrae, it seems much more likely to be due to the pull of the medius slips. It occurs in the third to sixth cervical vertebrae in European and other races (e.g. Punjabi (R.C.S.Mus. 631 A), Abyssinian Negro (R.C.S.Mus. 1257 A), and Ptolemaic Egyptian (R.C.S.Mus. 1265.12)), and may be found, either unilaterally or bilaterally as in man, in the gorilla (fourth, fifth, sixth cervical vertebrae), orang (third and fourth) and chimpanzee (fourth and fifth cervical vertebrae).

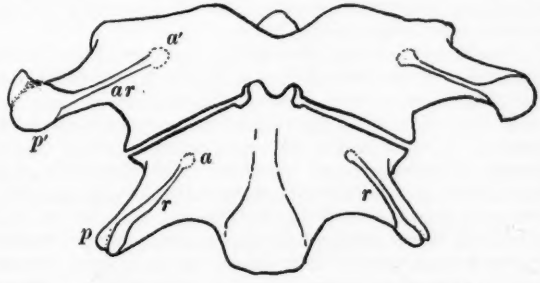

Fig. 2. Anterior aspect axis and atlas, showing anterior (*a*, *a'*) and posterior (*p*, *p'*) tubercles and the scalene ridges (*r*, *ar*).

(d) Axial and atlantal slips of Sc. medius

From the rudimentary, almost obsolete, anterior tubercle of the axis (*a* in fig. 2) a usually quite well-defined ridge (*r*) slopes downwards and outwards upon the antero-superior aspect of the transverse process to reach the single (and morphologically, the posterior) tubercle (*p*) upon the tip thereof; here the ridge broadens somewhat and terminates at a very faint groove, lateral to which the M. levator anguli scapulae occupies the tubercle. This ridge, which is borne by the morphological equivalent of the intertubercular (so-called costo-transverse) lamella of the lower cervicals, gives origin to the axial slip of the medius, the definition of whose inner margin is often rendered troublesome by the deeper prevertebral fibres and by the variable degree of development of the anterior intertransverse muscle between axis and third vertebra.

The pre-arterial limb of the atlantal transverse process is triangularly prismatic, with a posterior surface smoothed by the vertebral artery, and with antero-superior and antero-inferior surfaces which meet in front at a ridge (*ar* in fig. 2). In favourable instances this ridge may be traced from the front of the lateral mass, at, or close to, the site of the obsolete anterior tubercle, outwards and slightly downwards to the antero-inferior tip of the large posterior tubercle, i.e. to the site of origin of the upper-

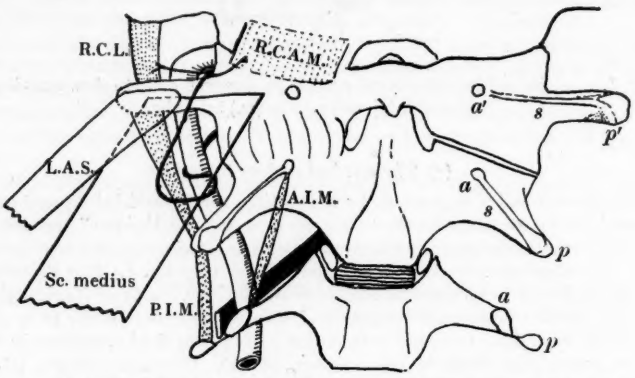

Fig. 3. Diagram to show relations of atlantal slip of scalenus medius (represented as transparent), Lettering as before; intertransverse muscles dotted; nerves in solid black.

most digitation of the levator: it gives origin to the atlantal slip of the medius, this fasciculus being overlapped in its upper and outer corner by the levator when the latter is moderately substantial (see fig. 3).

Manifestly in both axis and atlas the scalenus medius retains unaltered its peculiar morphological position on the intertubercular lamella, for notwithstanding authoritative statements to the contrary (e.g. Quain (6), Cunningham (2), Gray (3), Buchanan (1)) the large knob at the extremity of the atlantal transverse process is wholly the morphological posterior tubercle and is *not* representative of the fused anterior and posterior tubercles of lower cervical vertebrae. This conception appears to have arisen from the bituberculate nature of the tubercle in the vast majority of specimens, but other forms also occur (arrowhead, club-shaped, etc.), all morphologically unimportant and all the direct result of muscle traction. The pre-arterial limb of the transverse process is costo-transverse in nature, and is, to some extent, preserved as an entity by the action of the scalenus medius. It would be interesting to know, therefore, whether the atlantal slip of the medius is wanting in cases where the atlas exhibits absence or deficiency of this limb.

(e) *Relations of atlantal slip*

To the outer side of the atlantal medius slip lies the first slip of the levator scapulae, overlapping a little when well developed; directly internal, separating it from the prevertebral muscles and immediately in front of the atlanto-axial capsule, lies a quantity of soft fibro-fatty tissue, which extends deeply to reach the vertebral artery, and is sometimes admixed with odd scattered muscular or ligamentous fibres, which may be merely anomalous or may represent degenerated remnants of the uppermost anterior intertransverse muscles. Deep to the scalene slip lies the posterior atlanto-axial intertransverse muscle, and internal thereto but on a slightly deeper plane, the atlanto-axial segment of the vertebral artery with the anterior primary division of the second cervical nerve immediately in front of its forward concavity. This nerve pierces the fatty areolar tissue at the inner margin of medius and curves outwards across (rarely through) that slip to effect its union with its cranial fellow, curving downwards to meet it (see fig. 3). The appearance of C 2 anterior to the vertebral artery may seem surprising in view of its known position posterior to the vessel, but the difficulty is largely one of confusion of morphological with descriptive terminology.

Actually the nerve (ant. prim. div.) is dorsal to the artery throughout its course, and emerges in correct morphological alignment with its more caudally situate fellows, i.e. lying on the atlantal costo-transverse lamella between anterior and posterior tubercles. Descriptively, its course is as follows:

First lying in close contact with the back of the atlanto-axial capsule, apparently off the neural arch and covered by the inferior oblique, it curves thence successively round the back and outer side of the artery, covered laterally by the levator and splenius colli, and comes to lie directly anterior to the vessel which it separates from the atlanto-axial intertransverse muscle and, more anteriorly, the atlantal slip of the medius; finally, turning forwards at the inner edge of the scalene, it emerges through the fatty tissue to bend outwards across the muscle into the first loop of the cervical plexus.

No observations can be offered from the present enquiry as to the innervation of scalenus medius by the second spinal nerve.

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REVIEWS

Problems of Relative Growth. By JULIAN S. HUXLEY, M.A. (London: Methuen & Co., Ltd.) 1932. Pp. xix + 276, 105 figs. Price 12*s.* 6*d.* net.

This presentation of the problems of relative growth improves with acquaintance. Pézard in 1918 introduced the term "heterogonic" to describe the growth of an organ which increased at a different rate from the body as a whole. Huxley has seized on this notion of heterogonic growth. One would think that biology no longer holds possibilities for the philological inventor infatuated with pleonasms, for heterogonic was used by the botanist to describe the phenomenon presented by "pin-eyed" or "thrum-eyed" primroses, and by the zoologist for a particular form of alteration of generations in lower forms of life. The author takes the formula $y = bx^k$, where y is the size of an organ, x that of the remainder of the body. The value of y when $x = 1$ is b. The relative increase of y with regard to x is represented by the exponent k. If $k = 1$, the body and the organ increase in size at the same rate. If k is greater than 1, the organ grows more rapidly than the body. Conversely if k is less than 1, the organ grows less rapidly than the body. Huxley traces the alterations in the value of k for particular organs in various living forms ranging from bacteria and plants to Man.

As Huxley frankly admits his own mathematics are "regrettably deficient." Like the modern technocracist he loves to substitute logarithmic paper for the ordinary squared paper. Neither squared paper nor logarithmic paper, neither curves nor formulae necessarily clarify the understanding. He who knows not the formula for simple interest understands the significance of the statutory halfpenny per shilling per month on a redeemable pledge. He who knows not the formula for compound interest has an excellent grasp of the method of computation of interest adopted by certain usurers. A digression is immediately suggested: whether the modern biologist knows too little mathematics or too much. The mathematician in biology and physiology has in many cases deadened his originality, lost his ingenuity and mistaken a curve or formula, which at best is only a form of intellectual shorthand, for a new law in biology. Has not Aristotle said of animals that "they differ greatly from one another in their growth towards maturity. For instance, man, when young has his upper part larger than the lower, but in course of growth he comes to reverse this condition" (*Historia animalium*, II, 1). This is a clear statement of the principle underlying heterogonic growth. Far too often mathematical truths are confused with theorems in probability, and the latter, even when yielding results plotted out to five so-called "significant" figures and skew curves, do not necessarily facilitate the formation of correct judgments as a result of clear understanding of the biological problem under consideration.

Huxley has given himself, heart and soul, to the mensuration of growth and he has revived, restored and rejuvenated the older conceptions of metabolic gradients, growth gradients and growth potentials. He is at his best when dealing with the antlers of the deer and those invertebrate forms such as the fiddler-crab (*Uca pugnax*) and stag-beetle (*Lucanus cervus*) with which he is so familiar as a first-hand experimenter. Engrossed as he is in the mathematical method, Huxley is apt to ignore the contributions of such pioneers as Ostwald and Brailsford Robertson who first regarded growth as an autocatalytic physico-chemical reaction. He ignores the inter-relation of growth and behaviour pattern. He excludes the physiological outlook. For instance, Wertheimer has studied the behaviour pattern in young

mice, rats and guinea-pigs. Rats and mice, when new-born, are relatively insensitive to thyroxin, insulin and adrenalin, whereas the new-born guinea-pig is almost as sensitive as the adult. New-born mice and rats resist asphyxia; guinea-pigs do not. Temperature regulation is present in the guinea-pig at birth, but does not appear in the mouse or rat until the seventh day. Mere mensuration of these forms apart from considerations of their typical metabolic characters is not adequate.

From an entirely different approach H. A. Harris, pursuing the researches of Anthony and Coupin on the index of cerebral value, has shown that the rate of growth of the brain is related both to the behaviour pattern of the new-born and the degree of skeletal ossification. Animals which walk at birth have not only a high degree of ossification in the hind limb but also a brain which will increase but little in size from birth to adult life. On the other hand, animals which are born naked and helpless have a low degree of ossification in the hind limb and the postnatal growth of the brain is considerable. On the few occasions that Huxley does venture into biochemical realms he is apt to be unfortunate. He puts forward with reserve the thesis of Perkins that glutathione is associated with growth-potential. Since glutathione exists in maximal amounts in the region of the gonads in the embryo and foetus it is obviously difficult to accept this thesis.

Huxley follows the changing values of k in many cases. He analyses several forms in which the growth-gradients in the component parts of the limb vary markedly. In particular the examination of the growth gradient in the regenerating limb of the invertebrate yields results of great interest. He suggests that the reduction in value of k is concerned rather with the limitation than the speed of growth. The equation is of interest when applied to such cases of reversal of growth as are seen in starvation and old age; it is still more interesting in those cases presenting both increase of skeletal growth and alteration of bodily proportions in the young animal kept at constant weight by relative starvation, as in the experiments of Child, Champy and C. M. Jackson.

In the section dealing with heterogonic growth and hormones too much attention is paid to the mensuration of Hammett on thyroidectomised rats and too little to the experiments of Hammar who has shown the compensatory mechanisms that can be brought into existence in such cases. Hammett's classification of the organs of the body as regards differential sensitivity to thyroidectomy does not differ sensibly from the earlier conception of "master-tissues" or from the four types of skeletal, neural, lymphoid and urogenital growth described by Scammon and Jackson.

The last chapter, in which is discussed the bearing of heterogonic growth on other branches of biology, is a real contribution to the comparative aspects of growth. The changing mosaic of proportional parts is used both to warn the systematist and to suggest a solution of certain modifications independently of the Darwinian or Lamarckian concept. Huxley claims that alterations in dynamic growth-gradients may allow selection and mutation to affect various organs in a correlated fashion. This brings the growth-gradient into line with genetic factors which are known to control the rate of developmental processes, particularly in the embryo. The consideration of the degree of overgrowth in a part, or conversely, of reversal of growth, in its bearing upon the possibilities of survival of a given animal in a constant or changing environment yields an approach to the problems of evolution which is new and refreshing.

The book is profusely illustrated and forms a valuable introduction to variation and differential growth. It is a worthy successor to the books of Vernon, Donaldson, D'Arcy Thompson, Champy, Jackson, and Scammon and Calkins.

Growth. By the late JAMES LORRAIN SMITH, M.D., LL.D., D.Sc., F.R.S., Professor of Pathology, University of Edinburgh. Edited by J. S. HALDANE, C.H., M.D., F.R.S. (Edinburgh: Oliver and Boyd.) 1932. Pp. vi + 135. Price 6*s.* net.

Prof. J. S. Haldane, moved by friendship and intellectual sympathy, has made possible the publication of this book which the author had been unable to complete owing to his illness and death.

The book is a statement of the views at which the author had arrived by thinking hard and long on the various phenomena of growth of living organisms.

Growth is a procession in which cells divide meristically and in the production of the cell generations the progenitors disappear. So the process continues until the increase reaches the adult limit and differentiation is complete. Growth is due to the nature of the living cells, to the influence of all the other functioning and dividing cells and to the external environment. In this nexus it is not possible to disentangle cause and effect. At all times and at all stages of growth from the impregnated ovum to maturity the striking feature of growth is the co-ordinated maintenance of structure. This idea is an extension of the principle first enunciated for physiology by Claude Bernard. The problem of anatomy and pathology is the unravelling of the relations upon which this co-ordination depends. This book is devoted to the exposition of these relations so far as they are known in the various tissues of the body. A chapter is devoted to malignant growth and Prof. Haldane adds a concluding chapter summarising the preceding chapters and stating their philosophical implications.

Gray's Anatomy, Descriptive and Applied. Edited by T. B. JOHNSTON. Twenty Fifth Edition. (London: Longmans, Green & Co.) 1932. Pp. xvi + 1478. Figs. 1303. Price 42*s.* net.

This Twenty Fifth Edition of Gray's Anatomy is the second which bears the marks of the learning and industry of its most recent editor, Prof. T. B. Johnston. The book has now an unbroken history of nearly three-quarters of a century which, if not unique, is certainly remarkable. The present editor has attacked his gigantic task with amazing zeal and has not only maintained but made certain the continued eminence of this great monograph of Anatomy. The Section of Embryology is a book in itself. It includes all the recent advances in that subject affecting human anatomy and is lucidly presented. In the latest edition the editor has revised more specifically the section devoted to Surface Anatomy. We admire the editor for his courageous industry and congratulate him on the success which has attended his efforts. This book is a monument to British Anatomy.

Lehrbuch der Histologie und Histogenese. Von JOSEF SCHAFFER. Dritte Auflage. (Leipzig: Verlag von Wilhelm Engelmann.) 1933. Pp. viii + 576. 640 figs. Price: Geheftet R.M. 18. Gebunden R.M. 20.

The recent years have witnessed the publication of several important monographs on histology, evidence of the great success achieved by investigators in this field. To these is now to be added the third edition of Schaffer's well-known textbook. Ten years have elapsed since the second edition was published and the great advances made in histology have obliged the author to make alterations on almost every page, to rewrite whole chapters and to change fundamentally several of the earlier histological conceptions which until recently appeared well-founded.

In incorporating the new work the author has preserved the qualities that gave distinction to the earlier editions. The opening section on the blood enables the author to discuss the problems of cell structure, the reactions of cells, and histogenesis without making an abstraction of cytology and thus separating it from the rest of histology.

The author has included all the recent work on reticulum, the connective tissues, ductless glands, lung, liver, neuroglia, placenta, etc. but, in order to keep the text approximately within five hundred pages, has omitted the excellent account of the microscope which appeared in the earlier editions. This excellent book keeps, however, the brief but valuable historical introduction and the useful bibliography. The illustrations are extremely good.

Excitability. A Cardiac Study. By W. BURRIDGE, D.M., M.A. (Oxon.), Professor of Physiology; Lucknow University. (London: Oxford University Press.) 1932. Pp. ix + 208. 15 figs. Price 16*s.* net.

A New Physiology of Sensation. By W. BURRIDGE, D.M., M.A. (Oxon.), Professor of Physiology; Lucknow University. (London: Oxford University Press.) 1932. Pp. vi + 70. Price 6*s.* net.

The author reviews and interprets his extensive studies of cardiac behaviour as observed when the concentrations of the salts in the perfusing fluids is varied in different ways. His interpretation leads him to oppose the general trend of physiology in so far as this tends to identify the property of excitability with the response. The author is led on the contrary to infer that all biological phenomena are characterised by a series of events in which the excitable process precedes and is responsible for the response. The stimulus is not a mere trigger effect but something which adds energy to the reacting system and indeed further studies have led him to distinguish two forms of the excitable process and two kinds of response.

The excitable process arises from the potential energy of a salt-colloidal system—the kinesiophores. The size of the colloidal particles will determine through adsorption whether the salts increase or diminish in the surrounding aqueous medium. Experiment has revealed that calcium determines the size of the colloid particles and the reversibility of the change depends on potassium phosphate. These considerations have led to the fundamental equation; $H + L = T$. Where H is the varying concentration of the salts and L the varying size of the particles or freshness of the tissue and T is the response. T is a fixed quantity i.e. the response can never exceed a certain value. H and L are variables and apparently antagonistic in the sense that the more there is of one the less there must be of the other, but really they are synergic and neither can ever have zero value. These fundamental statements of biological phenomena are applied to a host of subjects in a most ingenious and interesting fashion.

Amongst the problems discussed are chronaxie, fatigue, the action of alcohol, double nerve supplies, sensation colour vision, and neurological and psychological theories, etc.

As an example H and L are interacting variables and thus there would be an optimum concentration of each at which say our mental processes, etc. would be what we ordinarily consider them to be but on either side of this there would be states in which H and L would differ widely and this activity would follow quite anything we are ordinarily accustomed to. Thus the author is led to find a basis for a tripartite division of mind and finds in modern psychology not only justification for such a subdivision of mental processes but points out how difficulties can be overcome and how further progress and rectification of existing ideas follows from the application of his own hypothesis.

The Races of Man. Differentiation and Dispersal of Man. By ROBERT BENNETT BEAN, M.D., Professor of Anatomy, Univ. of Virginia. The University Series. (Highlights of Modern Knowledge.) Physical Anthropology. The University Society. Inc. New York. To be obtained from the publishers only. Issued in various bindings and prices vary accordingly.

This is a vigorously written and readable account of some aspects of Human Biology. The first four chapters touch upon the zoological position of man and trace briefly his evolution and the unfolding of some of his special attributes. The remaining six chapters are devoted to the identification of racial differences, the differentiation, dispersal and other problems of racial Anatomy. The Text is illustrated by maps, diagrams and excellent pictures of different racial types. As a volume intended for general education it seems excellent.

Handbuch der Anatomie des Kindes. Edited by Drs KARL PETER, GEORG WETZEL and FRIEDRICH HEIDERICH. Vol. II, pt 3. (Munich: Bergmann.) 1931. Pp. 305–728, 168–423 figs. Price 88 marks.

The third section of the second volume of this extensive and ambitious work on the anatomy of children is devoted to the completion of the description of the blood vascular system, together with two large sections on the skeletal system and the nervous system.

Prof. Dragendorff of Griefswald is responsible for the vascular system, and he has collected a body of statistics relative to the growth changes in the arteries and veins of the trunk and the limbs such as is brought together in no other text book. The dimensions of the great arteries are given at the various ages and the variation with sex is carefully analysed. The histology of the vessels and the changes with age in the amount of elastic and muscular tissue is discussed and the pertinent age changes are analysed. Prof. Wetzel of Griefswald gives a detailed description of the umbilical vessels and the changes taking place after birth. Only four pages are devoted to the lymphatic vessels, an index of the work still to be done in this field.

Prof. Hasselwander of Erlangen contributes 170 pages to the skeletal system. The happy combination of anatomical presentation and radiographic interpretation which has characterised the whole of his work makes this section of extreme value. Hasselwander and Köhler have been the two pioneers in the fundamental correlation of Anatomy and Radiology. Since 1910 Köhler's *Grenzen des Normalen und Anfänge des Pathologischen im Röntgenbilde* and Hasselwander's *Die Bedeutung des Röntgenbildes für die Anatomie* have largely determined the rate and type of progress in this field. Hasselwander gives a particularly lucid account of the development of the skeleton illustrated with radiographs and microscopic sections. The detailed description of the age changes and epiphyses in the normal and the mildly abnormal child is very complete. The growth changes in the skull are depicted by illustrations and statistical tables.

Prof. Siwe of Lund describes the gross and minute anatomy of the nervous system in the child. In addition to the gross anatomy the growth changes are presented in convenient form; both histological structure, myelinisation and the possible significance of differentiation in the various areas of the cortex are considered. The main features of the peripheral nervous system and sympathetic system in the child are briefly dealt with.

The extensive bibliography together with the wealth of illustration make this book of fundamental importance in the study of paediatrics. Information which is often required by the orthopaedic surgeon and pathologist no less than by the

anatomist has been brought within the compass of this book. It is a matter of congratulation that the first anatomical textbook which has attempted a coherent blending of the facts gained from radiographic and pathological examination as distinct from routine anatomical dissection should be a textbook devoted to the anatomy of children.

Grundzüge einer Konstitutionsanatomie. By WALTER BRANDT. (Berlin: Julius Springer.) 1931. Pp. 382, 135 figs. Price 29·80 gold marks.

This presentation of the fundamentals of constitutional anatomy by Prof. Walter Brandt of Cologne breaks new ground. It is a laudable attempt to synthesise into a whole the work in the various fields of bodily habitus, constitution and racial characters, attention throughout being focussed on the underlying biological basis. At the same time from the analytical side the problems of constitution are dissected in terms of structure, growth and differentiation. The comparative treatment of "Entwicklungsmechanik" is traced in animal forms ranging from the invertebrates to Man with numerous references to analogous processes in the plant world.

The presentation of our state of knowledge as regards breeding of horses and cattle is related to the different types of bodily habitus in Man. The main phenomenon of intersexuality in amphibians and birds is discussed in terms of the endocrine glands with special reference to the particular time at which the endocrine factors reach their maximum potency.

The wealth of illustration in this book together with the broad view of problems in constitution throughout animate forms cannot fail to remind one of the distance traversed since Andrias Vesalius described the anatomy of the dissected corpse.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY, WITH A NOTE ON THE MORPHOLOGY OF THE CHOROIDAL ARTERIES

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INTRODUCTION

There has never, as far as I am aware, been any controversy as to the source from which the lateral geniculate body receives its blood. Duret published in 1874 (1) the results of his researches into the blood supply of the brain generally and states that the lateral geniculate body receives its blood solely from the posterior cerebral artery, either directly, or indirectly *via* the posterior choroidal branches. His results have been confirmed or contradicted for many regions by later workers (Heubner, Kolisko, Beevor, Aitken, Stopford, Shellshear), but his description of the vascularisation of the geniculate body has been practically unchallenged. In the same year Heubner (2) announced the findings of his own researches, anatomical and pathological, in this field, but, while he contradicts Duret on many points, he asserts that the posterior cerebral artery alone is concerned with the lateral geniculate body.

In 1891, Kolisko (3) studied the distribution of the anterior choroidal artery in its relation to the posterior limb of the internal capsule. He was concerned mainly with the internal capsule and mentions the lateral geniculate body in only a few of his injections. There was, apparently, no doubt in his mind that the posterior cerebral artery was chiefly involved, and in injection 12 he discusses the relation of the anterior choroidal artery to the lateral geniculate body thus: "ein Injectionsstreif, welcher um das Corpus geniculatum laterale aussen herumzieht und bis ans Unterhorn reicht...." In no case did he obtain injection of the lateral geniculate body through the anterior choroidal artery. In addition, Kolisko collected two cases of occlusion of the anterior choroidal artery: in one, the obstruction was at the origin of this vessel, in the other, at its terminal branches. In the former, of which he gives the clinical findings, there is the specific statement that there was no interference with vision; in the latter, clinical data were unobtainable.

In 1905, von Monakow (4), in his discussion of the blood supply of the brain, states: "So wird z.B. das Corp. genicul. ext. nicht nur von einem Seitenast der hinteren Hirnarterie, sondern auch von Abzweigungen aus der dem Carotisgebiet entstammenden Art. chorioidea mit Blut gespeist" (p. 1085). This interesting statement is not, however, further expanded.

The whole problem of cerebral arterial supply was reinvestigated by

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Beevor(5) in 1909. As the result of his study of nearly one hundred brains, Beevor was able to publish very complete charts of his findings, and these have been the accepted standard until recent times. In twenty-three cases the anterior choroidal artery was injected individually, and in four of these the lateral geniculate body was reached, but not in the remaining nineteen. This fact Beevor records, but he finally concludes that the lateral, like the medial, geniculate body receives its entire blood supply from the posterior cerebral artery; nor does he attempt to explain his four discordant results.

Recently, Dr Ivy McKenzie of Glasgow reported a case wherein the post-mortem findings threw doubt upon the generally accepted view that the lateral geniculate body was entirely vascularised by the posterior cerebral artery. He communicated his anomalous results to Prof. Elliot Smith of University College, London, and it is to the kind suggestion of the latter that I am indebted for the opportunity of making this fresh study of the problem. This case is, I believe, the first of its kind to be described and, although Dr McKenzie is reporting it in full elsewhere, I shall give the history here because of its importance:

Mrs C. 41 years: always enjoyed perfectly good health, although slightly nervous for the last two years. One child, six years, and baby born on 28. iv. 31. No miscarriages. Children both healthy. Although nervous for two years she had no pains or disability of any kind. In the beginning of March, 1931, two months before the birth of the baby, she felt her right hand become weak and shaky. She also became sleepless and went off her food. The hand became worse and in a week or two the right leg began to drag, and about the beginning of April the eyes became affected and there seemed to be a film before the eyes.

After the birth of the child she became worse. When she was seen on 2. v. 31 she complained of pain at the back of the neck and said that she felt as if the upper part of the eyesight was affected when she looked at objects above her own height. She could not hold things comfortably and she could not recognise objects in her hands when her eyes were closed. Tactile and spatial discrimination were defective in both right hand and foot, and cutaneous sensation was dull all down the right side of the body. The reflexes were exaggerated both in the arm and the leg, and there was paresis of the right side of the face. This paresis was definitely of the organic type (Babinski, Clonus).

There was no ocular palsy; the fundi were normal; there was contraction of the field of vision. The Wassermann reaction was positive. Anti-syphilitic treatment caused improvement. She was able to walk without any appearance of lameness and by the end of June the power had been restored to the right hand for all ordinary purposes. She still complained about her eyesight, became very depressed and ultimately took her own life by lysol. The eye chart by Dr Meighen showing the visual defect was made on the day before she took her own life.

The eye chart referred to shows great visual loss in the upper half of both fields, but is more complete towards the left on both sides. There is, in addition, slight concentric diminution of the lower field of vision on both sides. The lower nasal field of the right eye is also considerably contracted. It must be emphasised, however, that the macula has been almost completely spared; it has been involved only to a slight degree at its upper border.

At post-mortem there was found a syphilitic endarteritis of both anterior choroidal arteries. The distribution of the latter to the posterior limb of the internal capsule and to the cerebral peduncle would be sufficient to account for the paresis and anaesthesia (I have confirmed the findings of Kolisko to that extent), but what is far more important as far as we are concerned was the finding of a clear-cut area of degeneration affecting the *lateral aspects of both lateral geniculate bodies.* Now, according to the work of Brouwer and Zeeman, the lateral portion of the lateral geniculate body corresponds with the projection of the lower quadrants of both retinae towards the same side, i.e. with the upper quadrants of both visual fields towards the opposite side. Since the upper half of each visual field has almost completely gone, we can regard the interference with vision as a bilateral superior homonymous quadrantic hemianopia, corresponding with the bilateral involvement of the lateral aspects of the lateral geniculate bodies; further, since the defect is more marked towards the left than the right, it is safe to assume that the right lateral geniculate has undergone a more extensive degeneration than the left. The arterial involvement was clearly unequal, because the paresis and anaesthesia are recorded as having been on the right side only.

As far as I am aware, this is the first recorded case of a visual defect associated with the anterior choroidal artery. In Kolisko's first case no interference with vision was found; but it must be emphasised that there is no record of any perimetric charting. Apparently, there was merely no complaint on the part of the patient of deficiency of sight. Here, then, are two cases of similar pathological import; one with the record of no visual defect, the other having both subjective and objective interference with sight.

These are the only two accounts I can find of undoubted anterior choroidal arterial interference. Henschen (6, 7, 8), it is true, has collected an enormous number of cases of visual lesions, but, although some of his clinical and pathological findings leave no doubt that the anterior choroidal artery was involved, in no case is there mention of an examination of the individual vessels, and so, for our purpose, his valuable collection is useless.

MATERIAL AND METHOD

In nearly every investigation of cerebral arterial supply the various arteries have been injected with a coloured mass, followed by the examination of transverse, horizontal and sagittal sections of the whole brain.

Duret, in his pioneer work, apparently combined injection of the vessels with the dissection of their surface distribution, but he did not follow the arteries through the brain substance for fear of rendering the structures through which they passed unrecognisable. He was content to cut sections through the whole brain and identify individual vessels by matching adjoining sections. The same technique was employed by Heubner, Kolisko and Beevor.

Aitken (9), in a series of beautiful illustrations, has demonstrated that arteries can be traced through the brain substance to their terminations without destroying the structures through which they have passed. In this investigation—dealing as it does with the blood supply of a comparatively superficial structure—we are not concerned with following our vessels any great distance into the brain itself. At the same time, as the field of enquiry was increased to include the complete distribution of the anterior choroidal artery (the results will be published later), it was found that Aitken's method could be employed with advantage, since it obviously is more exact than the former.

The dissections were performed upon twelve human hemispheres which had been preserved in formalin for varying periods, consequently it was impossible to inject them satisfactorily with coloured gelatine mass. In the case of the first six hemispheres, the dissection was made without injection; subsequently, it was found possible to inject the anterior choroidal artery quite successfully with indian ink by the aid of a syringe and a very fine hypodermic needle, the artery then being tied off with silk to prevent any reflux escape of the ink. This naturally rendered dissection much more simple, and the results were satisfactory in that they completely confirmed the findings of the first dissections and also threw some light upon the results of previous investigators. In particular, they explained the reason for Beevor's failure to inject the lateral geniculate body *via* the anterior choroidal artery in nineteen cases out of twenty-three. This I will discuss more fully later.

After the arteries had been dissected in their surface distribution, their terminal disposal within the geniculate body was studied. The block of brain containing the latter was cut in sections 1 mm. thick with a safety razor blade by hand. These sections were stained individually with alum-haematoxylin and eosin and cleared with oil of wintergreen. Examination with a binocular microscope by strong transmitted light displayed the end arteries in relation to the cell masses and fibre bundles.

As a corollary to the investigation of the human condition, the blood supply of the lateral geniculate body was studied in a limited, but representative, phylogenetic series. This series comprised six anthropoid, two lemur, four sheep, two Marsupial, two crocodile and two *Sphenodon* hemispheres.

The methods employed were the same as in the human: the vessels were first examined in their surface arrangement and the terminal distribution was subsequently ascertained by means of thick, cleared sections. In all cases, except that of the sheep, the thick sections were checked against ordinary thin sections stained for cells and so error was largely eliminated. In the case of the sheep, although no such sections were available, it is felt that there is very little chance of mistake, as the picture seen in the thick sections was quite clear. (These have since been checked against thin sections stained for cells and found to correspond accurately.) The *Sphenodon* brain was, naturally, too valuable to be dissected, so the arterial distribution was studied

from the surface only. Fortunately, I had access to a series of transverse sections which served as a valuable guide.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN MAN

A. The anterior choroidal artery

I do not propose to discuss here the various modes of origin and distribution of this vessel. These have been fully described by previous workers and reference to the papers by Duret, Heubner, Henle (10), Kolisko, and others will suffice for the purposes of those who wish to follow the subject further; I shall go more fully into this matter in a subsequent publication. For the present, it is enough to state that I have observed every variation described by these investigators except that of complete absence of the anterior choroidal artery. In no case, in a series of some eighty hemispheres examined, was it impossible to find a vessel which had the origin, course and distribution of the anterior choroidal artery.

This vessel usually arises from the internal carotid artery at a varying level between the posterior communicating and middle cerebral arteries. From its origin it passes backwards and medially across the optic tract, when it runs along the medial aspect of the latter until it reaches the level of the anterior pole of the lateral geniculate body. Here it divides into a varying number of branches most of which turn rather abruptly laterally and, recrossing the optic tract, enter the inferior horn of the lateral ventricle to reach the antero-inferior part of the choroid plexus (fig. 1).

Throughout its course this artery gives origin to branches which are distributed to the structures close to which it runs. These have been described in some detail by previous workers, but, although my findings do not coincide in all respects with theirs, I shall not enter upon a minute description of the complete distribution of this artery at present; a brief account will not, however, be out of place.

The most striking of these branches are those which are said to enter the superficial surface of the optic tract for its supply in its course posteriorly. Aitken has pointed out that these vessels often do not perforate the optic tract, but "wrap themselves around either its medial or lateral aspect." Actually, the branches which perforate the optic tract are few and fairly large. They supply a few small twigs to the tract, but the main vessels pass dorsally into the base of the brain to reach the posterior limb of the internal capsule and the optic radiation. The branches which "wrap around" laterally are distributed to the base of the brain to reach the corpus striatum, and some pass laterally to the temporal pole, the uncus and the posterior part of the amygdaloid nucleus. Of those which run medially, some pass to the pes pedunculi and through the latter to the substantia nigra, some pierce the base of the brain while most of the remainder "wrap around" the medial aspect of

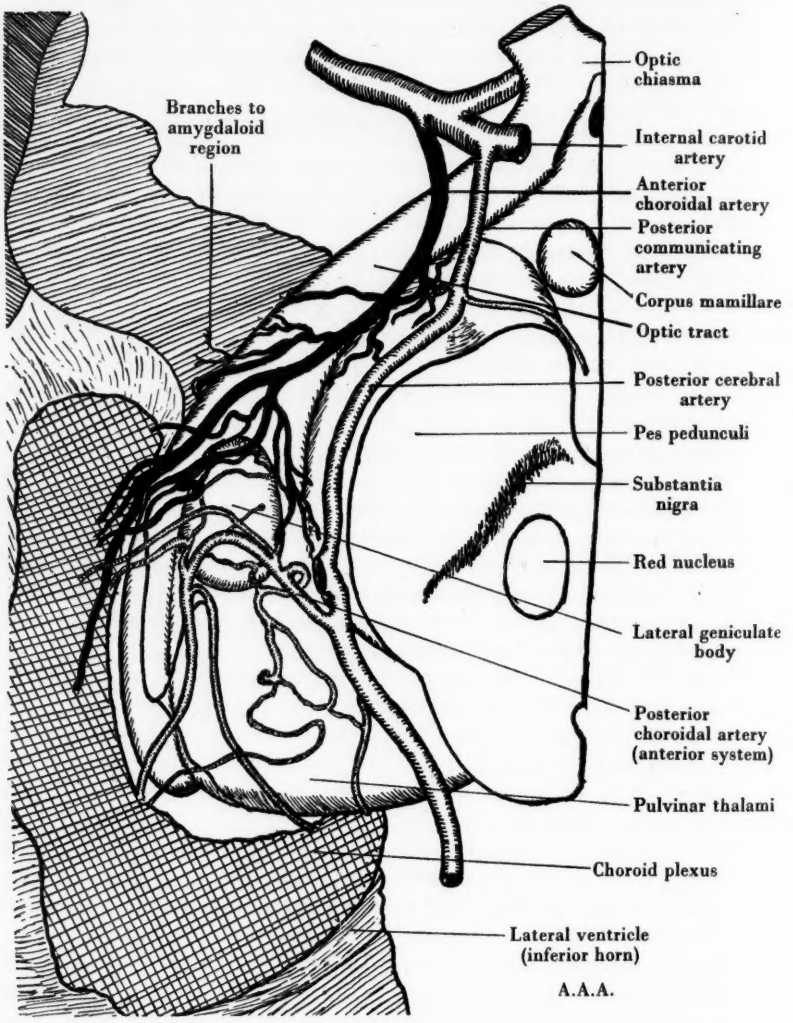

Fig. 1. Drawing of the general origin, course and distribution of the injected human anterior choroidal artery; note how the injection has missed some of the terminal branches of the artery.

the optic tract to enter its dorsal surface. It is these last which are the true arteries of supply to the tract. In addition to these vessels, there are rich anastomoses in the pia mater with branches of the middle cerebral, posterior communicating and posterior cerebral arteries.

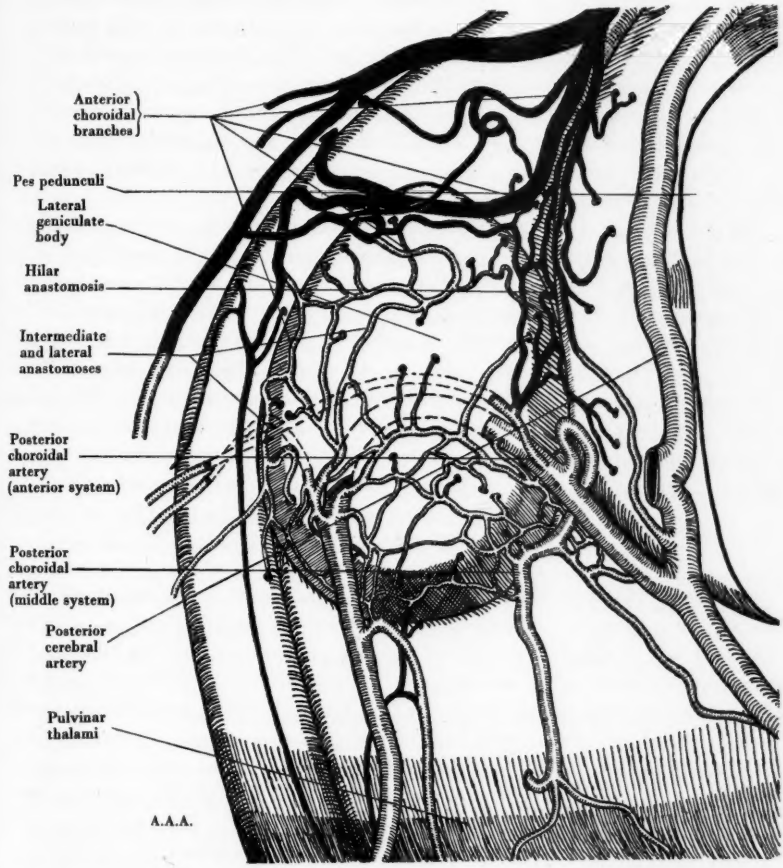

Fig. 2. The distribution of the anterior choroidal and other arteries over the surface of the lateral geniculate body; from the same specimen as fig. 1.

The terminal divisions of the anterior choroidal artery vary greatly in size and number in different specimens. Often a large branch turns medially to join the anastomosis on the crus, whilst one vessel very constantly enters the stria terminalis in which it runs posteriorly for some distance. Apart, however, from the branches to the lateral geniculate body, the majority of the remainder pass to the choroid plexus (fig. 2).

With regard to the part played by the anterior choroidal artery in the vascularisation of the lateral geniculate body, a very constant arrangement was observed which held, with minor variations, for every dissection. Two, three or more medium-sized branches arise from the terminal divisions of this artery and take part in the anastomoses subsequently to be described (fig. 2). Usually two or three of these arise medially and pass posteriorly in the vallecula which lies medial to the geniculate eminence. (This eminence, it will be remembered, corresponds only with the most lateral part or tail of the geniculate body; the vallecula is the hilum, and a portion of the ganglion lies more medially still, against the crus, forming a medial elevation.) These medial vessels, then, enter into a very rich anastomosis with branches from the posterior cerebral and posterior choroidal arteries.

As the anterior choroidal divisions pass laterally anterior to the geniculate body a further series of small vessels runs posteriorly from them and back over the geniculate eminence to join the intermediate and lateral anastomoses. These anterior branches may all arise separately, or wholly, or in part, from a common stem. Whatever their mode of origin, however, they invariably proceed to these final anastomoses. In addition to the above, one or more large vessels take origin from the anterior choroidal divisions after they have passed some way back in the choroid plexus. These arteries leave the lateral ventricle and run medially to reach the lateral aspect of the lateral geniculate body.

B. Posterior choroidal arteries

Duret, in his description of the choroidal arteries, mentions a postero-lateral and a postero-median choroidal artery. He states that the anterior choroidal artery supplies the antero-inferior part of the choroid plexus, and that the postero-lateral "completes the vascularisation of the choroid plexus." The postero-median artery is described by him as passing directly backwards on the side of the pineal body to which it gives some twigs. It soon divides into two branches which supply the choroidal membrane and plexus of the third ventricle. Charpy describes only one posterior choroidal artery (11), and states that, "Cette artère est relativement atrophiée"; he also mentions a median choroidal artery which may arise from the posterior cerebral artery or from the superior cerebellar and which passes to the choroid plexus of the third ventricle. Presumably, it corresponds with Duret's postero-median artery.

Leaving out of account the postero-median, or median, choroidal artery as not coming within the sphere of the present enquiry, I find that I cannot support the statement that the posterior choroidal artery is "relatively atrophied"; on the contrary, I can usually distinguish three, and sometimes as many as five, large vessels which pass from the posterior cerebral artery to reach the choroid plexus. These, then, must correspond to Duret's single

postero-lateral choroidal artery. In addition, the posterior choroidal vessels show a steady increase in number and complexity as we ascend the phylogenetic scale. Careful study of these vessels forces me to the conclusion that they are the persisting representatives of a large number of transverse arteries which had been interconnected by several longitudinal anastomoses. The remaining vessels are the surviving portions of some of the stem arteries and parts of the original network which have been picked out from the many intermediate paths available. The varying modes of origin, and the very diverse courses of distribution pursued by these vessels can be an expression of no other circumstance.

The functional end arteries have remained constant throughout; it is only the stem arteries and the vessels of distribution which have varied. Indeed, Duret makes this striking observation (concerning cerebral arteries in general): "C'est là du reste, une loi générale pour les artères du cerveau: leur origine est souvent très-variable, mais leur champ de vascularisation est constant" (p. 81). This principle is a remarkable anticipation of the work of Stopford (12) and Shellshear (13–18), but was never pursued further by Duret. Shellshear in particular, as the result of his numerous investigations of the blood supply of the cerebral cortex of a large number of animals, and especially of Man, has always insisted upon the functional constancy of vascularisation of the brain, and was the first to place this hypothesis upon a firm anatomical basis (13, 14, 15, 16, 17, 18). In the same relation it is interesting to note that Guyot, in 1825 (19), made a somewhat similar statement.

In all these dissections it was possible to distinguish three main systems of posterior choroidal arteries to which I shall refer as the anterior, middle and posterior systems. The anterior and middle systems alone are concerned in the blood supply of the lateral geniculate body; I was totally unable to discover any branches proceeding from the posterior system to this ganglion.

The anterior system takes origin from the posterior cerebral artery at a variable point, usually anterior to the sulcus lateralis of the peduncle (fig. 2). Characteristically, it is composed of one fairly large vessel supplemented by one or two much smaller ones which may arise apart, but often take origin in common with the main vessel. These pass forwards or backwards until they reach approximately the level of the centre of the geniculate body when they turn laterally and, crossing the latter, enter the inferior horn of the lateral ventricle, posterior to the anterior choroidal divisions, and reach the choroid plexus. The largest of these vessels is fairly constant, but the smaller ones vary considerably. In the choroid plexus they all join in the general anastomosis, but we need not pursue their course further at present.

The anterior system plays an important part in the formation of the series of anastomoses over the surface of the lateral geniculate body. Close to its origin it gives a large number of small branches to the rich medial anastomosis, while, as it proceeds laterally, it similarly reinforces the intermediate and

lateral anastomoses. These branches may arise in part or solely from a common stem, but they pass constantly to their destinations. Some of the smaller twigs pass directly into the substance of the geniculate body, while frequently a further branch arises from the choroidal divisions and pursues a recurrent course out of the ventricle to reach the lateral anastomosis posteriorly.

The middle system usually consists of a single, fairly large vessel arising from the posterior cerebral artery just posterior to the anterior system, but it may take origin in common with it. However it arises, this vessel runs forwards or backwards until it reaches a level just posterior to the posterior pole of the geniculate body, when it turns laterally to pass behind the latter. After a variable lateral course, the artery bends posteriorly in a wide curve and, passing dorsally around the thalamus, enters the central part of the choroid plexus.

In its passage posterior to the geniculate body, the artery generally divides into a number of branches which subserve its terminal distribution in the choroid plexus. These terminal branches appear to vary considerably, but in actual fact, if a number of dissections be compared, it is found that the mean of their combined courses is fairly constant. In particular, either the main trunk or one of its branches almost invariably goes out of its way to pass anteriorly, close to the posterior pole of the geniculate body, before sweeping around posteriorly and dorsally to reach the choroid plexus.

The reason for describing what is apparently a single artery as a system is now clear, for the distribution of its terminals can only be regarded as the expression of an originally large series of vessels passing from the posterior cerebral artery to the central part of the choroid plexus, and the longitudinal anastomoses between them. What remains is the survivor of portions of this network, most of which has disappeared.

The branches from this system are numerous, but we need only discuss those to the geniculate body. Briefly, they arise from the main trunk and its branches as these pass laterally. They are especially rich medially where they join the medial anastomosis; more laterally they are less numerous as they pass forward to complete the intermediate and lateral anastomoses. These twigs may arise individually or in bunches, and a large number enter the substance of the geniculate body directly.

The posterior system of posterior choroidal arteries comprises, usually, one or more fairly large vessels which arise from the posterior cerebral artery and pass to the choroid plexus. These vessels also are very variable in their mode of origin and in the course they pursue; the remarks made concerning the middle system apply equally well here and need not be repeated. Briefly, they pass dorsally around the thalamus close to the mid-line to reach the more dorsal and anterior parts of the choroid plexus of the lateral ventricle. They take no part in the blood supply of the lateral geniculate body and require no further description here.

C. The arterial anastomoses over the surface of the lateral geniculate body

The proportion of vascular supply to the geniculate body undertaken by any one of the systems just described (anterior choroidal, anterior and middle systems of posterior choroidal) is very hard to assess accurately on account of the intricate network of vessels over its surface. One cannot doubt that such rich vascularisation is evidence of the great functional importance of this ganglion, and I hope to show that the distribution of these arteries bears a constant relation to that functional differentiation which we already know to exist from the researches of Brouwer and Zeeman, Minkowski and Le Gros Clark.

The vascular network can be resolved into three main longitudinal series of anastomoses which have been referred to as the medial, intermediate and lateral anastomoses. Further, an anterior, middle and posterior series of transverse anastomoses can be described, but, as these have neither the phylogenetic nor the functional significance of the former, they can safely be neglected (fig. 2).

For the sake of simplicity, we can regard the anterior and middle systems of posterior choroidal arteries as being only posterior cerebral, for this differentiation has no importance as far as the lateral geniculate body is concerned. Of the three, the medial anastomosis is by far the richest. It receives important support from the anterior choroidal artery, but at least two-thirds of its blood comes from posterior cerebral branches. This vascular network ramifies in the vallecula or hilum and gives a very rich supply to this region, both medially and laterally. The intermediate and lateral chains of anastomosis are sometimes hard to distinguish, and they dwindle away as we pass laterally over the eminence. In this movement, laterally, we find that the anterior choroidal contributions become increasingly more substantial, while those from the posterior cerebral artery correspondingly diminish. So, when we reach the lateral border, we find that practically the whole of the blood is supplied by the anterior choroidal artery (taking into account, especially, the strong reinforcements from the choroid plexus).

Now it is possible to say that the anterior choroidal artery is distributed to the anterior, but especially the lateral parts of the ganglion, while the posterior cerebral artery reaches the posterior, but especially the medial regions. The region of the hilum has by far the richest blood supply, which comes from both sources, but mainly from the posterior cerebral artery.

D. Distribution of the arteries within the lateral geniculate body

In the thick clarified sections through the geniculate body (fig. 3 A and B) the terminal distribution of the end arteries is easy to follow. These vessels pass into the ganglion from the surface, but while the majority end within

the nucleus, there are some which pass right through and then accompany the fibres of the optic radiation. The more detailed drawing of the vessels shows that the terminal twigs all end accurately within a particular cell lamina. Each cell lamina can be regarded as a distinct nucleus having its own discrete blood supply. Further, it can be seen that a vessel in its course through the geniculate body gives branches which are distributed to corresponding areas of adjoining cell laminae from the ventral to the dorsal border. In addition, in association with the lateral eversion of the human geniculate body, a distinct hilum has been produced, and from this hilum the vessels tend to radiate dorsally, medially and laterally to reach their final objectives; there are, however, a few arteries which pass into the lateral eminence almost at right angles to the surface to vascularise the lateral part of the ganglion.

We have already seen that the medial anastomosis lies within and on the lips of the hilum and, in accord with the much greater number of vessels in this region, we find that the number of terminal twigs distributed to this intermediate quadrant of the geniculate body is greater than to the more medial and lateral segments. Further, this intermediate part is supplied from two sources, from the anterior choroidal artery and from the posterior cerebral artery, although the latter contributes the greater support. The tail, or eminence, receives the major portion of its blood from the anterior choroidal artery and the medial part more from the posterior cerebral artery.

Brouwer and Zeeman (20–22) have shown that this intermediate quadrant is almost entirely macular in its projection, while the medial and lateral portions are predominantly non-macular; the upper part of the retina is projected medially and the lower half laterally. Thus, it is obvious that the macular quadrant, which is functionally the most important, has by far the greatest blood supply and, in addition, draws its nourishment from two sources. While this double blood supply has probably been evolved in accordance with the greater functional activity of the part, it certainly must compensate to a large extent for interference with either of its sources, but especially with the anterior choroidal artery, thus tending to spare the macular projection.

Reverting to Dr Ivy McKenzie's case we can now see why, although the anterior choroidal artery was affected, the macular interference was at a minimum, while the non-macular field was more extensively involved. Fig. 3 C is a drawing taken from a slide of one of the geniculate bodies in the case in question. Here it will be seen that the area of degeneration of the cells is strictly limited to the lateral part of the ganglion in accordance with both the vascular lesion and the perimetric recording, but the macular projection quadrant is scarcely encroached upon.

It is possible to go further than this, however, for there is evidence to show that the distribution of the terminal vessels is even more precise than has so far been described.

Minkowski (23) and Le Gros Clark (24) have both shown that corresponding

retinal areas are projected in alternate cell laminae of the two geniculate bodies, e.g. crossed fibres end in what Le Gros Clark calls **1** *a*, **2** *b* and **3** *b*, while uncrossed fibres terminate in the remaining laminae **1** *b*, **2** *a* and **3** *a*, and it follows from the work of Brouwer and Zeeman that adjoining parts of

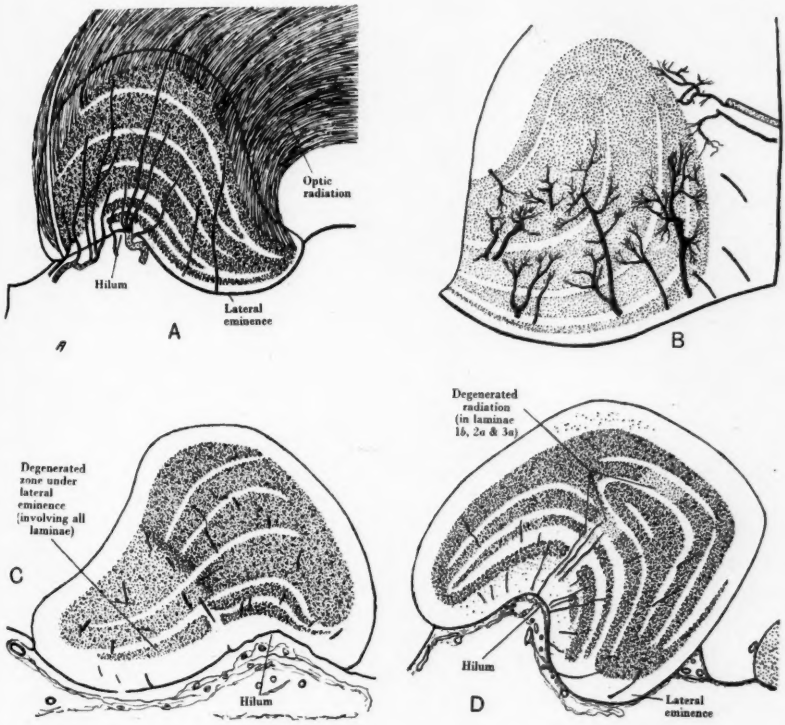

Fig. 3. *A.* Thick section of the human lateral geniculate body; note the rich vascular supply to the hilar region and the poorer supply medially and laterally.
B. Thick section of a human lateral geniculate body illustrating the termination of the end arteries in the cell laminae.
C. Right lateral geniculate body from slide kindly lent by Dr Mackenzie showing atrophy of the cells in the lateral part consequent upon interference with the anterior choroidal artery.
D. Section of the lateral geniculate body of a *Macaque*. This is from an animal which was operated upon by Mr Penman of St Thomas's Hospital, a lesion being inflicted in the temporal side of the macula of the homolateral eye. Kindly lent by Professor Le Gros Clark.

neighbouring cell laminae are related to corresponding areas of both retinae. Thus, if a small area of laminae **1** *a*, **2** *b* and **3** *b* be related to the nasal field of the opposite eye, then the intervening parts of laminae **1** *b*, **2** *a* and **3** *a* correspond to the temporal field of the homolateral eye.

Fig. 3 D represents a drawing made from a slide of the geniculate body of an ape. In this animal a lesion had been experimentally produced involving the temporal side of the macula of the homolateral eye. The circumscribed areas of degeneration in laminae 1 *b*, 2 *a* and 3 *a* are clearly depicted. We can be fairly certain that the intervening sections of the remaining laminae are related just as closely to the nasal side of the opposite macula. It is important to note how the vessels radiate from the hilum, and how some of them are passing right through this fan-shaped area of degeneration. We have already seen that as a vessel passes through the cell laminae it radiates from the hilum in the same way as this degenerated area, and as the whole macular projection zone does in Brouwer's diagrams. Further, we have seen that in its passage through the geniculate body each individual artery gives off twigs to the adjoining parts of neighbouring cell laminae as it passes through them. There can be very little doubt, then, that *each individual end artery is as closely related to each individual retinal projection area within the lateral geniculate body as are the very cells which subserve this projection.* In this relation, it is of interest to note that the same arteries which nourish these cells frequently accompany their axones for some distance into the optic radiation.

To summarise the condition in Man:

(1) The anterior choroidal artery plays a large and constant part in the blood supply of the lateral geniculate body.

(2) The anterior choroidal artery is related to the lateral aspect of this ganglion, while the posterior cerebral branches are distributed more medially and posteriorly.

(3) The area of greatest functional importance—the macular projection area—has by far the richest blood supply, and this supply is drawn from the double source of the anterior choroidal and the posterior cerebral arteries.

(4) There is evidence to show that the end arteries within the lateral geniculate body are distributed in close relationship with the projection of the visual fields in this ganglion.

The discrepancy of Kolisko's first case is now apparent. The patient was a sick old man with hemiplegia who died of pneumonia a fortnight later. It is unlikely that such a patient would complain of a visual defect which was related only to the upper quadrant of both fields of vision towards the opposite side and in which the macula was little involved if at all. Such a visual defect may have existed, but was unobserved in the absence of any perimetric investigation.

We have seen that the anastomoses over the geniculate body are very rich. It is clear that these are sufficient to ensure injection of the ganglion *via* the posterior cerebral artery. This explanation is the only one which can be adduced in explanation of the failure of previous workers to inject this body. There is no doubt that the anterior choroidal artery plays a very constant part in the blood supply of the lateral geniculate body.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN APES

The injected or uninjected vessels were dissected in the six hemispheres of three apes. The anterior choroidal artery was examined in eighteen hemispheres which included brains from *Lagothrix*, *Papio*, *Cercopithecus* and *Macacus*. In all of these cases the artery was constantly present, well developed and easily demonstrated. There were minor variations which corresponded with the human condition.

A. The anterior choroidal artery

This vessel, in its passage from the internal carotid artery to the anterior pole of the lateral geniculate body, is so similar to the human that there is no necessity to repeat the description. When it reaches the geniculate body, however, the condition, although comparable, does not conform exactly to our previous description (fig. 4). In the human it was seen that the main course of the anterior choroidal artery was into the choroid plexus in the lateral ventricle, while the branches which passed posteriorly to take part in the medial, intermediate and lateral anastomoses were of minor importance. In the ape we find that the branches to the geniculate body are much larger, while the choroidal divisions have become relatively reduced in size. Further, it is the large terminals to the geniculate body which now course posteriorly over the surface of the latter and replace the intermediate and lateral anastomoses. The branches which enter into the medial or hilar anastomosis are likewise increased in importance.

B. Posterior choroidal arteries

The condition of the posterior choroidal arteries in the ape conforms fairly closely to Duret's description of a postero-lateral and a postero-median artery for Man. The former arises from the posterior cerebral artery in the same position as did our anterior system in Man, and it runs across the lateral geniculate body to reach the lateral ventricle. Before this occurs, it enters into such a free anastomosis with the anterior choroidal artery that the two vessels lose their individuality, and it is impossible to distinguish them with certainty.

The postero-median artery follows the same plan of origin and distribution as in Man, but I have never seen this vessel arise from the superior cerebellar artery as described by Charpy. Between the postero-lateral and postero-median arteries are many small vessels which run from the posterior cerebral artery to the choroid plexus. These are certainly the predecessors of the middle and posterior systems in Man, but they have not attained the human degree of development because the functional demands made upon them are not such as to require a greater volume of blood than they already supply. Of all these, the only artery concerned with the lateral geniculate body to any

extent is the postero-lateral. This, as we have seen, crosses the geniculate body and usually joins the anterior choroidal artery by a free anastomosis. Some branches from the posterior cerebral artery, as in Man, pass directly to the medial anastomosis.

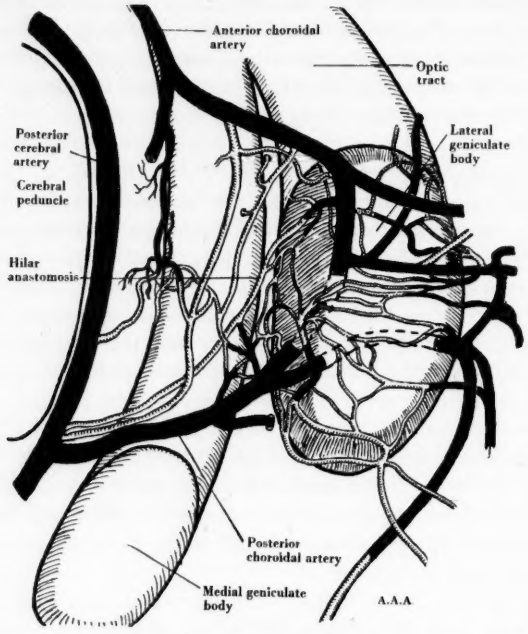

Fig. 4. Distribution of the arteries over the lateral geniculate body of a Guinea Baboon (*Papio papio*); the injection has flowed freely into the posterior choroidal artery.

C. Anastomoses over the surface of the lateral geniculate body

These can be dismissed with a short description. The medial anastomosis is again very rich and is probably supplied equally from the anterior choroidal and posterior cerebral arteries. The intermediate and lateral anastomoses are replaced by some of the main terminal divisions of the anterior choroidal artery which, in place of the small vessels of communication of the human condition, join the posterior choroidal vessel by a very free channel.

D. Distribution of the arteries within the lateral geniculate body

The condition here is so similar to the human that little further description is required. The end arteries pass into this ganglion chiefly from the hilum, but, in accordance with the greater degree of eversion of the geniculate body

in the apes, the vessels fan out from this region much more markedly than in Man. The end arteries also terminate just as accurately in the cell laminae and are quite as certainly related to the retinal projection areas.

To summarise the condition in apes:

(1) The anterior choroidal artery supplies a much greater proportion of the lateral geniculate body than in Man.

(2) It is still closely related to the anterior, and especially the lateral aspects, and plays a much greater part in the vascularisation of the hilar, or macular, area. The posterior cerebral branches are here relegated to a more subordinate position.

(3) The distribution of the end arteries within the body is comparable with the human condition, and is related to the retinal projection areas. The slight variation is to be attributed to the greater degree of eversion of the anthropoid geniculate body.

(4) The terminal branches of the anterior choroidal artery, as in Man, nearly all join branches of the posterior cerebral artery, but the anastomosis is much more free.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN THE LEMUR

The condition was examined on both hemispheres of the brain of a *Lemur variegatus*. Although the arrangement of the arteries was, in the main, the same as in the higher Primates, the variations found called for the investigation of the condition in a larger series than I have at my command.

The lateral geniculate body of the lemur presents an anomalous condition which is not directly comparable with the state of affairs in higher animals. This has been investigated by Woollard (25, 26), Pines (27) and Le Gros Clark (28) and reference to these authors will suffice to define the present state of our knowledge.

It already appears from this single lemur brain that the arteries to the geniculate body are as far removed from the general line of Primate evolution as is the lemur itself. It is felt that the condition of the arteries is closely correlated with the aberrant evolution of the geniculate body, but it has been decided to defer their description until more exact information is available.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN THE SHEEP

The state of affairs was examined in four hemispheres and was found to be constant in all.

A. The anterior choroidal artery

This vessel was constantly present and of sufficient size to permit of its injection with some difficulty. It arises in its usual place from the internal carotid artery and passes posteriorly and dorsally along the optic tract. In

its course posteriorly (fig. 5), the vessel lies first at the infero-posterior border of the tract and then gradually crosses the latter until it lies at its centre at the anterior pole of the diencephalon (which here corresponds with the anterior pole of the lateral geniculate body). Thence it passes obliquely across the latter until it reaches the antero-dorsal pole, where it turns medially and joins the posterior cerebral artery.

Throughout its course its branches are distributed as in Man, to the amygdaloid region, the optic tract, the choroid plexus and the pes pedunculi. In its oblique passage across the geniculate body it gives many branches which pass into the latter and into the diencephalon, and many others which anastomose with similar branches from the posterior cerebral artery. It will be noticed that it is the main trunk of the anterior choroidal artery which passes across the diencephalon to anastomose finally with the posterior cerebral artery, while the actual choroidal arteries are, even more than in the ape, of subsidiary importance.

B. Posterior cerebral artery

It is difficult to speak of posterior choroidal arteries in the sheep because they play very little part in the supply of the geniculate body. While a few small branches cross the diencephalon to reach the plexus of the lateral ventricle anteriorly, the major posterior choroidal contribution lies much more dorsally, out of our immediate field of enquiry.

The posterior cerebral artery arises from the junction of the posterior communicating and basilar arteries and runs obliquely dorsally across the pes to reach the groove between the medial and lateral geniculate bodies. Thence it again turns more obliquely and passes across the postero-superior angle of the diencephalon and so around the dorsal aspect of the latter to supply the choroid plexus and the posterior part of the cerebral hemisphere and to receive the termination of the anterior choroidal artery.

In its course it supplies branches to the pes, the medial and lateral geniculate bodies, the superior colliculus, and the diencephalon. In addition, there are several small branches for anastomosis with branches of the anterior choroidal artery.

C. Anastomoses over the surface of the lateral geniculate body

As will be seen from the illustration (fig. 5), these are by no means as complicated or as numerous as in the apes and Man. They are merely a series of small vessels which pass from the posterior cerebral artery to the anterior choroidal. The latter also has channels of communication with the middle cerebral and posterior communicating vessels.

D. The distribution of the arteries within the lateral geniculate body

The lateral geniculate body of the sub-Primates is formed of two distinct nuclei, dorsal and ventral. The latter is the more primitive, is developed from the subthalamus and is connected mainly with the tectum (Kappers (30), Le Gros Clark (29)). The dorsal nucleus is of later development, has evolved from the ventral nucleus of the thalamus proper and, in Primates, sends the

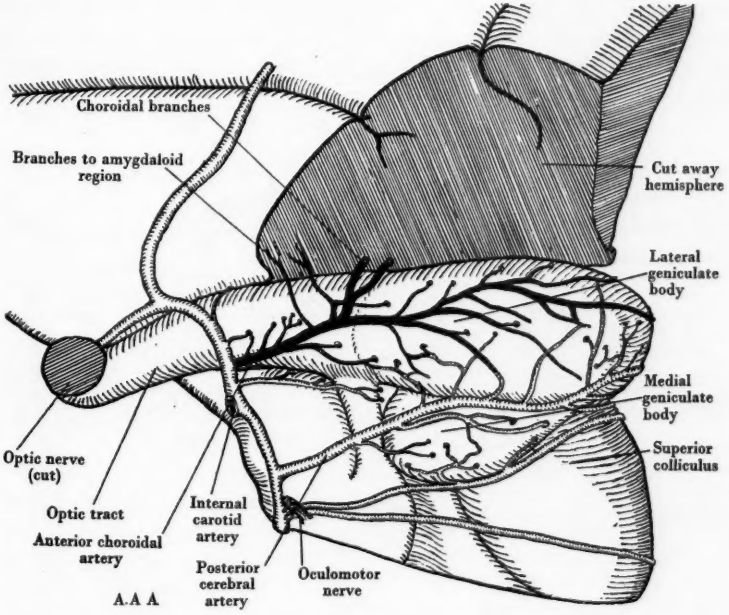

Fig. 5. Distribution of the arteries in the *sheep*. The anterior choroidal artery is injected.

majority of its efferent fibres to the area striata of the cerebral cortex. It is from the dorsal nucleus of lower animals that the complicated lateral geniculate body of the Primates has evolved, while the ventral nucleus is, in them, probably represented by the corpus pregeniculatum. Both dorsal and ventral nuclei are well developed in the sheep, but, as the details of their intimate blood supply are the same as in the Marsupial, I shall defer the discussion of these vessels until the condition in the latter has been described; the same description will serve for both.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN THE MARSUPIAL

The condition of the vessels was investigated in both hemispheres of a tree-kangaroo (*Dendrolagus*) and was found to be the same in both. This was checked by a series of *Dasyurus* sections stained for cells.

A. The anterior choroidal artery

This vessel was easily found and could be injected with some difficulty. It arises from the internal carotid artery as usual and passes dorsally along the centre of the optic tract. At the anterior pole of the diencephalon the vessel turns cranially and continues its dorsal course along the most anterior part of the diencephalon. Then it turns medially and finally anastomoses with the posterior cerebral artery (fig. 6).

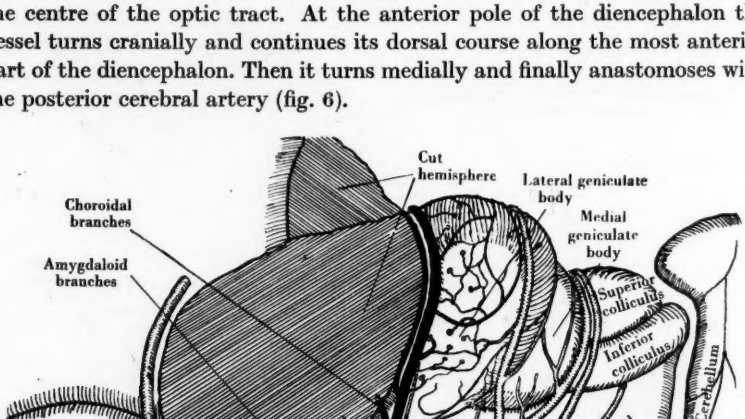

Fig. 6. Distribution of the arteries in the Marsupial (*Dendrolagus*), anterior choroidal artery injected.

The branches given off are exactly comparable with those observed in the sheep, i.e. to the amygdaloid region, the optic tract, the choroid plexus and the diencephalon whose most lateral border is here almost entirely overlaid by the lateral geniculate body. In addition, there are branches which anastomose with the middle cerebral, posterior communicating and posterior cerebral

arteries, the last over the lateral geniculate body. It will be seen that the main vessel is that which passes dorsally over the geniculate body to anastomose with the posterior cerebral artery; the actual branches to the choroid plexus of the lateral ventricle are, in the Marsupial, very minute.

B. Posterior cerebral artery

The posterior cerebral artery seems to acquire most of its blood from the basilar in this animal, and the posterior communicating artery is only a small vessel. This vessel passes dorsally across the pes and medial geniculate body to reach the caudal border of the lateral geniculate body. Here it at once turns cranially and continues its course dorsally over the centre of the geniculate body. It gives the usual branches to the pes, tectum, medial and lateral geniculate bodies. Also there are anastomotic twigs to the anterior choroidal artery over the geniculate body and, finally, the latter artery joins the posterior cerebral.

C. Anastomoses over the surface of the lateral geniculate body

These are as simple as those of the sheep and require no detailed description.

D. The distribution of the arteries within the lateral geniculate body

According to Tsai (31), the lateral geniculate body of the Marsupial is very well developed and consists of separate dorsal and ventral nuclei. I have been able to check these observations both in the thick sections and in a series of sections stained for cells.

Fig. 7 represents a series of drawings of thick sections through the lateral geniculate body with the dorsal and ventral nuclei represented in outline only. These sections show the relation of the geniculate body to the optic tract, and represent successively posterior levels passing from A to D. The anterior choroidal artery is drawn in black, and it can be seen that as we pass posteriorly and dorsally so the anterior choroidal artery ascends in the sections just as we observed from the surface dissection. At the same time the dorsal nucleus migrates in the same direction, and the close relation between the artery and the dorsal nucleus is very striking as we pass posteriorly; the artery maintains a faithful affinity to the course of its field of supply. The terminal twigs of the anterior choroidal artery pass into the dorsal nucleus but were never observed to reach the ventral. In fact, we may say that the anterior choroidal artery is the chief source of supply for the dorsal nucleus. Its branches, too, can be seen passing through the dorsal nucleus to accompany the optic radiation as in higher animals.

The branches of the posterior cerebral artery are just as closely related to the ventral nucleus, and the artery seems to pass upwards in the sections

in association with the increase in size of the ventral nucleus. There is however one striking difference. In all sections one or two branches of the posterior cerebral artery pass some distance dorsally in the optic tract until they reach the level of the interval between the two nuclei; then, passing medially in this interval, these branches give off twigs which reach, not only the dorsal aspect of the ventral nucleus, but also *the ventral part of the dorsal nucleus.*

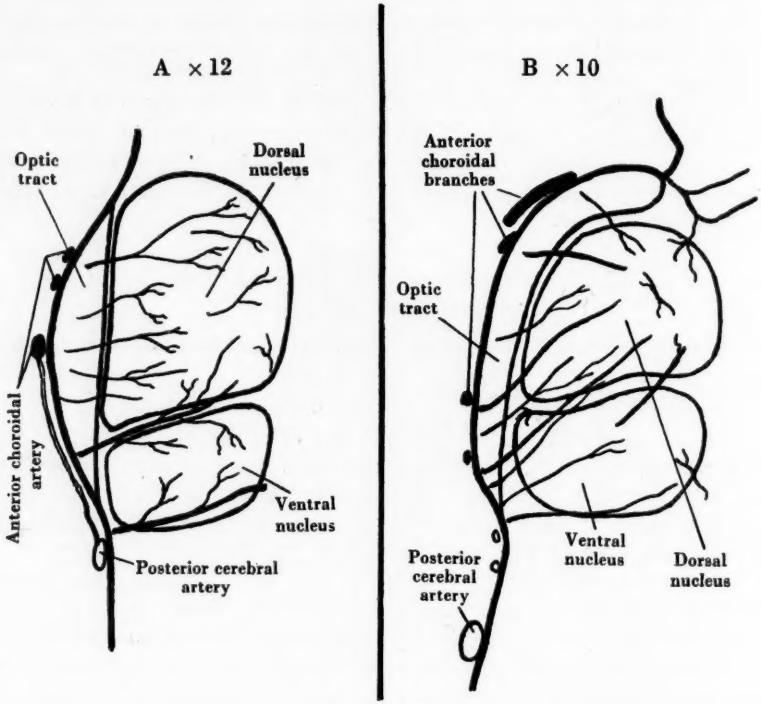

Fig. 7 (*A*, *B*).

Fig. 7. Terminal distribution of the end arteries within the lateral geniculate body of the Marsupial. *A*—*D*, sections running posteriorly, showing the relation of the anterior choroidal artery to the dorsal nucleus and the posterior cerebral artery to the ventral; note branches of the latter passing to the dorsal nucleus.

The ventral portion of the dorsal nucleus thus receives a double supply; partly from the anterior choroidal artery and partly from the posterior cerebral artery.

Now we know that the dorsal nucleus of the lower Mammals becomes the main nucleus of the Primates, and we also know that this latter ganglion has become everted during its evolution so that its more dorsal part comes to lie

laterally, and the ventral part lies medially. In between is the hilum which represents the axis of rotation.

In Man and the apes, we saw that the posterior cerebral branches supplied the medial aspect of the geniculate body and the anterior choroidal the lateral aspect, while the hilum received its supply from both arteries. The homology is complete, for the arterial distribution is the same, with the ventral part of

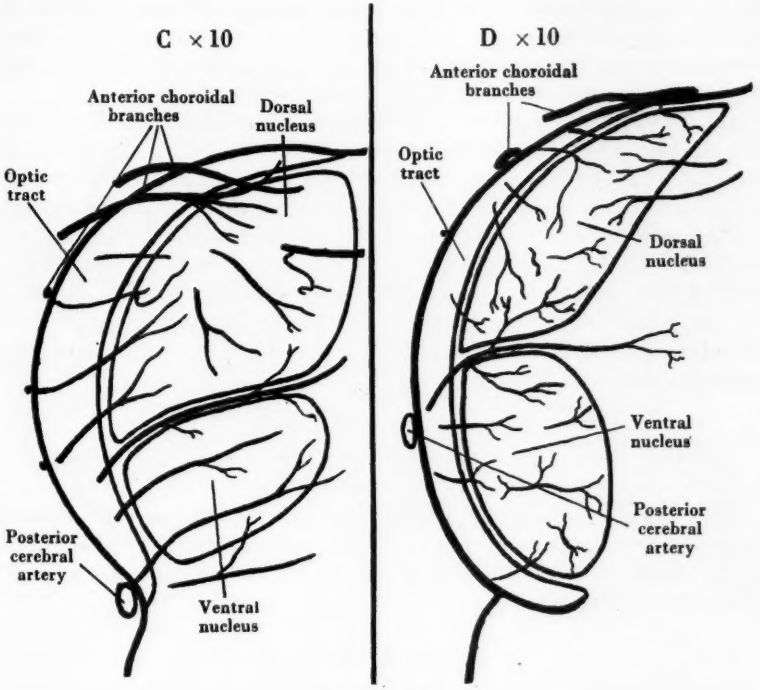

Fig. 7 (*C*, *D*).

the dorsal nucleus representing the medial border of the Primate geniculate body and supplied by the posterior cerebral artery; the next most ventral part is supplied by both arteries and represents the hilum, or axis of rotation, while the most dorsal part of the dorsal nucleus represents the lateral aspect and receives its supply almost entirely from the anterior choroidal artery.

The arrangement of the vascular supply in the sheep closely resembles that of the Marsupial.

To summarise the findings in the *Eutheria* and the *Metatheria*:

(1) The lateral geniculate body is divided into separate dorsal and ventral nuclei each of which has its own specific blood supply: the dorsal nucleus

receives most of its blood from the anterior choroidal artery, but its ventral part is vascularised by the posterior cerebral artery as well; the ventral nucleus is supplied solely by the posterior cerebral artery.

(2) The blood vessels are distributed in an exactly comparable manner to those in the Primates: the part of the dorsal nucleus which is supplied only by the anterior choroidal artery corresponds developmentally with the lateral part of the Primate geniculate body which also takes its blood from the anterior choroidal artery; the intermediate section, corresponding with the hilum, is vascularised by both vessels, and the most ventral part of the dorsal nucleus, which is the predecessor of the medial portion of the Primate geniculate body, is supplied by the posterior cerebral artery.

(3) The anterior choroidal artery is precisely comparable with its homologue in higher Mammals in the origin from the internal carotid artery, the course along the optic tract, the distribution to the tract, the geniculate body, the amygdaloid nucleus and pes, and in the termination in the posterior cerebral artery. The main difference is that, as we descend the phylogenetic scale, the vessel is progressively of less importance as a choroidal artery, because the choroidal branches become smaller; while the main portion of the vessel becomes more and more that channel which runs posteriorly over the lateral geniculate body to end in a free anastomosis with the posterior cerebral artery.

THE BLOOD SUPPLY OF THE LATERAL GENICULATE BODY IN THE CROCODILE

This was examined in both hemispheres of the brain of an Indian gharial. It was impossible to inject any individual anterior choroidal vessel, so the whole arterial system was injected with indian ink through the basilar and internal carotid arteries.

A. The anterior choroidal artery

For convenience of description, it will be useful, in the case of the crocodile and *Sphenodon*, to regard the internal carotid artery as dividing into cranial and caudal branches, as done by Hofmann (31*a*) and de Vriese (32, 33). The cranial branch is the anteriorly directed division of the internal carotid which gives rise to the middle cerebral artery, and is continued as the anterior cerebral artery. The caudal branch is the posterior cerebral artery of higher animals.

When we examine fig. 8, we can see that there is a system of tiny vessels which arise from the cranial artery, run posteriorly on the optic tract and terminate in the caudal artery. Further, this system supplies branches to the optic tract, the amygdaloid region, to the diencephalon (whose most lateral aspect is occupied by the lateral geniculate body) and also anastomotic twigs to the middle cerebral and caudal arteries. This network, then, is

certainly the predecessor of the anterior choroidal artery, and shows a fair amount of variation in the crocodile. On the right side of the brain it is represented by a rich network of tiny vessels, but, on the left side (that illustrated), it is more definitely a discrete artery. It may be objected that this vessel has no choroidal branches, but it must be remembered that in reptiles the lateral ventricle has no inferior horn—the choroid fissure is limited to the region of the foramen of Monro—and the choroidal branches of the caudal artery pass into this region and suffice for its requirements.

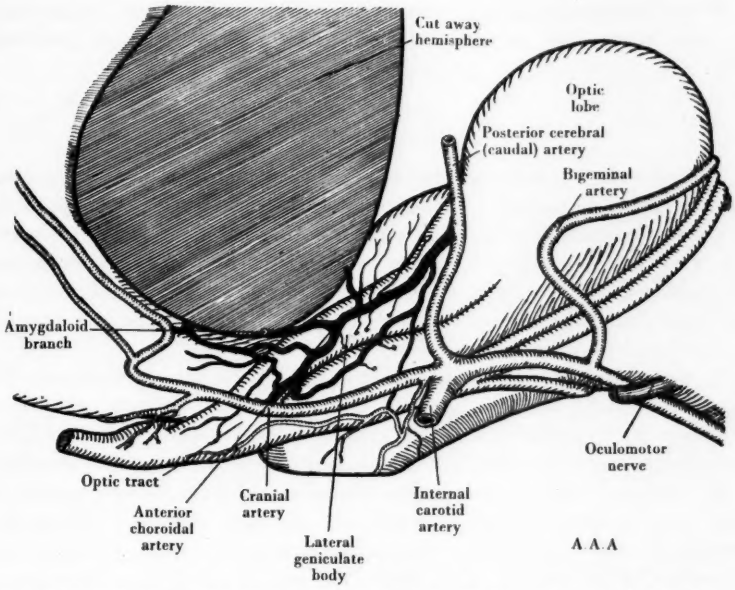

Fig. 8. Distribution of the arteries in the Indian *gharial*, the anterior choroidal artery is represented in black, but was not separately injected.

This condition will become clearer after we have examined the posterior cerebral artery in the crocodile and the arrangement in *Sphenodon*. In the meantime, it can be noted that this vessel satisfies all the criteria for homology with the anterior choroidal artery except that it has no connection with the choroid plexus.

B. Posterior cerebral (or caudal) artery

This vessel appears to take origin equally from the internal carotid and basilar arteries in this specimen. From its point of commencement it passes dorsally across the optic tract to reach the interval between the optic lobe and the cerebral hemisphere and supplies both. Finally it turns around the

postero-dorsal angle of the hemisphere and is distributed to the cerebral cortex. During its course it gives branches to the optic tract, the pes and to the choroid plexus of the third and lateral ventricles. In addition, it is joined in its course over the tract by the anterior choroidal artery.

Thus in the crocodile the anterior choroidal artery is not a true choroidal artery inasmuch as the choroid plexus is entirely supplied by the posterior cerebral (or caudal) artery. It should be noted that the anterior choroidal artery is very rudimentary and is closely related to the optic tract and especially the lateral geniculate body.

It was impossible, since all the arteries were equally injected, to ascertain the exact relation of the anterior choroidal artery to the lateral geniculate body.

THE *SPHENODON*

The material available was the injected brain of a *Sphenodon punctatum* and a series of transverse sections through the brain of another *Sphenodon* stained by Ranson's silver-pyridine method. As it was not desirable to destroy such a valuable specimen I merely examined the arteries in their surface distribution as far as could be done by gently pressing aside the hemispheres. For a portion of our description, then, we must be content to rely upon the excellent account given by Dendy (34).

In fig. 9, the internal carotid artery can clearly be seen to divide into cranial and caudal branches, and the basilar takes little, if any, part in the formation of the latter. The cranial artery passes anteriorly obliquely across the optic tract and, having given off the middle cerebral branch, is continued as the anterior cerebral artery. The caudal artery runs dorsally across the optic tract to enter the interval between the optic lobe and the cerebral hemisphere and is eventually dissipated by being distributed mainly over the surface of the latter. In its course the caudal artery gives branches to the optic tract, the optic lobe and cerebral hemisphere and a rich supply to the choroid plexus in the region of the foramen of Monro. It will be observed that there is no artery which can be described as being homologous with the anterior choroidal artery; that is, there is no single vessel which arises from the cranial artery, passes posteriorly along the optic tract and ends in the caudal artery.

Taking origin from the cranial division is a small vessel (indicated in fig. 9 in black) which passes dorsally between the optic tract and the medial aspect of the postero-inferior angle of the cerebral hemisphere and is then lost to sight. This artery gives twigs to the anterior part of the tract and some to the region of the amygdaloid nucleus. It is called the arteria cerebralis inferior by Dendy, and is described by him as passing to the region of the corpus striatum which it probably supplies. In addition, there is an anastomotic vessel between the middle cerebral and caudal arteries which

crosses the postero-inferior angle of the hemisphere and clearly gives twigs to the amygdaloid region, and there are twigs from the caudal artery to the posterior part of the optic tract.

If all these elements were fused to form one single artery or a small network stretching from the cranial to the caudal arteries, we should have precisely the same condition as exists in the crocodile. This hypothetical composite artery would arise from the cranial artery, would run posteriorly along the optic tract and would end by joining the caudal artery. Further, in its course posteriorly, it would supply the optic tract (and the underlying lateral geniculate body), the amygdaloid nucleus and the posterior part of the corpus

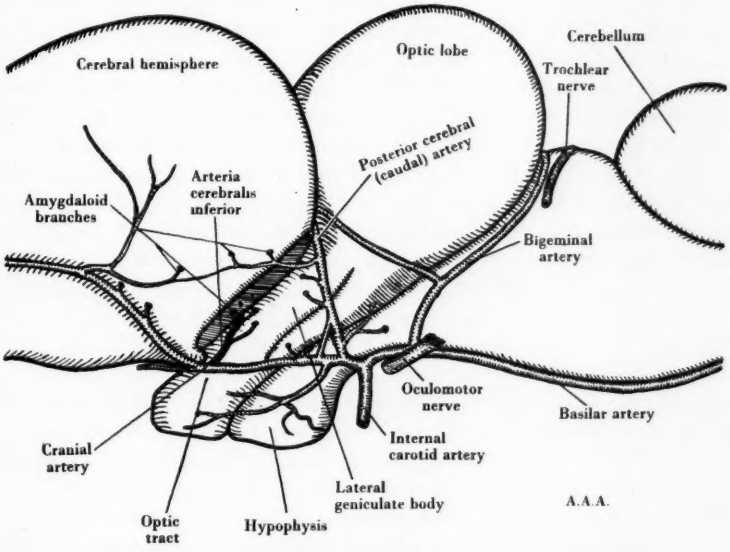

Fig. 9. Distribution of the arteries in the *Sphenodon*; the *arteria cerebralis inferior* is represented in black.

striatum and, in addition, would effect anastomoses with the middle cerebral artery. This is the condition found in the crocodile, and it is clear that in *Sphenodon* we have all the elements necessary to form a higher reptilian anterior choroidal artery, although there has, as yet, arisen no direct link with the choroid plexus. The anterior choroidal artery in the crocodile has been formed from both cranial and caudal divisions of the internal carotid artery; it is clearly a longitudinal anastomosis between the two in response to some specific demand.

Consider the development of the lateral ventricle, which can be regarded as having been drawn upwards and posteriorly between the two fixed points,

the foramen of Monro and the amygdaloid nucleus. In the course of evolution both the ventricle and the choroid fissure assume an arcuate form, while the posterior pole of the hemisphere bulges backwards over the optic tectum. While this is going on the caudal artery lengthens to maintain its field of supply and, as it comes to lie alongside the lengthened choroid fissure, it supplies more and more collateral twigs through the fissure to the plexus. At the same time the posterior portion of the anterior choroidal artery, which came originally from the caudal branch, is drawn posteriorly until it, too, comes to lie alongside the elongated choroid fissure. At this juncture the posterior part of the anterior choroidal artery is called upon to take some part in the nourishment of the choroid plexus (through its phylogenetically posterior cerebral, or caudal contribution). At this stage we have reached the primitive mammalian condition and the story of the formation of the anterior choroidal artery is complete.

In ascending the mammalian scale, in keeping with the increasing growth of the lateral ventricle and the growing functional demands of the enlarging choroid plexus, the anterior choroidal artery has progressively devoted more and more of its attention to the choroid plexus. In the Marsupial, the main trunk of the anterior choroidal artery ran posteriorly to join the posterior cerebral artery, while the choroidal branches were of subsidiary importance; in the sheep, in accordance with the greater development of the antero-inferior part of the choroid plexus, the choroidal branches were larger, although the main channel still ran posteriorly to end in the posterior cerebral artery; in the apes the antero-inferior part of the choroid plexus has become so important that the anterior choroidal artery is equally divided between the plexus and its union with the posterior cerebral artery (which takes place over the lateral geniculate body); in Man we reach the terminal phase in which, while fulfilling all its original vascular requirements (optic tract, amygdaloid nucleus, anastomosis with middle cerebral artery, pes), the major trunk is devoted to the now enormously enlarged antero-inferior part of the choroid plexus. The terminal union with the posterior cerebral artery is represented merely by the lateral, intermediate and medial anastomoses over the lateral geniculate body.

We have seen that the first rudiments of the anterior choroidal artery were observed in *Sphenodon*; we have also seen that throughout its phylogenetic evolution this artery has been closely related to the optic tract and, especially, the lateral geniculate body. Cairney (35) has described the diencephalon of *Sphenodon* and has distinguished a definite pars dorsalis. While there is a well-marked pars dorsalis diencephali in Reptiles, the Amphibia possess only a mere rudiment of this structure. Cairney has also described a lateral geniculate body which has definite dorsal and ventral nuclei and it is probable that the dorsal nucleus has differentiated from the pars dorsalis diencephali of the Reptiles, that is, from the general sensory or ventral nucleus of Mammalia. In *Sphenodon* we have the first rudiments of an anterior

choroidal artery associated with the first appearance of a dorsal nucleus in the lateral geniculate body (disregarding, in the meantime, the remainder of the field of supply of the artery).

The crocodile presents a rudimentary but definitely discrete anterior choroidal artery, but has it a dorsal nucleus to its lateral geniculate body? Huber and Crosby (36) describe a lateral geniculate body in the alligator, but do not state whether it is to be regarded as a dorsal or ventral nucleus or as both. The alligator is a more highly developed Reptile than *Sphenodon*, and its pars dorsalis is quite as well differentiated. I have had the opportunity of examining serial sections of the diencephalon of both the alligator and the crocodile, and it would appear that the lateral geniculate possesses both dorsal and ventral nuclei. In addition, Cairney has identified his dorsal nucleus with the lateral geniculate body described by Huber and Crosby. It thus appears that in the crocodile we have the first discrete anterior choroidal artery associated with a dorsal nucleus of the lateral geniculate body. In the Marsupial the problem is not so difficult, for we have seen the close relation of the anterior choroidal artery to the dorsal nucleus of the lateral geniculate body; the condition in the sheep is very similar.

The problem of the Primates is now simple. The anterior choroidal artery is devoted to the anterior and especially the lateral portion of the lateral geniculate body. This, as seen in the sheep and Marsupial, corresponds exactly with the field of supply of the most dorsal part of the dorsal nucleus.

SUMMARY AND CONCLUSIONS

1. The first appearance of the separate components of the anterior choroidal artery is found in *Sphenodon* in association with what is probably the first appearance of a definite dorsal nucleus of the lateral geniculate body.

2. In the crocodile these elements have fused to form a network of vessels which connects the two parent arteries—the cranial and caudal divisions—along the optic tract. The crocodile probably has a definite dorsal nucleus to its geniculate body. At this stage in phylogeny the anterior choroidal artery takes no part in the supply of the choroid plexus.

3. In the Marsupial the artery has reached a more typical stage in its development. Although the main vessel still runs posteriorly across the geniculate body to reach the posterior cerebral artery, there are some small branches which are swept aside into the now much elongated choroid fissure to reach the choroid plexus. Further, in the Marsupial the anterior choroidal artery bears a definite relation to the dorsal nucleus which is maintained throughout all successive stages.

4. In the sheep the conditions are practically the same as in the Marsupial. The increased growth of the cerebral hemispheres, associated with a consequent enlargement of the lateral ventricle and the choroid plexus, is expressed in the greater size and importance of the choroidal branches of the anterior

choroidal artery. The relation of the latter to the dorsal nucleus of the lateral geniculate body remains the same. At the same time the posterior choroidal arteries have similarly enlarged in response to the greater functional demands made upon them.

5. In the ape the anterior choroidal artery is an important vessel. Its terminal branches (not including those to the amygdaloid nucleus, pes and internal capsule) appear to be equally distributed between the now greatly enlarged choroid plexus and the lateral geniculate body. The lateral geniculate vessels anastomose, as ever, with the posterior cerebral branches which, on account of the enormous development of the choroid plexus, are mostly represented in the posterior choroidal artery. The relation of the anterior choroidal artery to the lateral geniculate body, which corresponds almost entirely to the dorsal nucleus of lower animals, is exactly comparable with that found in the latter.

6. In Man the cerebral hemispheres and the choroid plexus have so greatly enlarged that the main part of the anterior choroidal artery is devoted to the choroid plexus. The terminal branches course posteriorly over the lateral geniculate body as small twigs in the intermediate, medial and lateral anastomoses to join the posterior choroidal arteries. The latter have enlarged so much that they can be separated into three main systems of posterior choroidal arteries. The relation of the anterior choroidal artery to the lateral geniculate body (dorsal nucleus only) is the same as in the ape.

7. Finally, in Man and in apes, the distribution of the end arteries in the various laminae of the lateral geniculate body is precisely correlated with the discrete areas of functional representation of the retina.

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THE DEVELOPMENT AND MYELINATION OF THE POSTERIOR LONGITUDINAL BUNDLE IN THE HUMAN

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THE posterior (or medial) longitudinal bundle owes its interest partly to its early phylogenetic and ontogenetic development, and partly to the varied and numerous connections that indicate the importance of its functions. This bundle must not be confused with the dorsal longitudinal bundle of Schütz which runs through the central grey matter of the entire brain stem close to the floor and connects with the nuclei of all the cerebral nerves(1): it must also be distinguished from the faisceau longitudinalis medialis of Winkler(2), also called the faisceau fronto-occipitalis, that lies lateral to the head of the caudate nucleus.

The tract is present in all Vertebrates, and in Fishes, Amphibians and Reptiles it represents one of the largest bundles of the brain stem(3). In the human embryo it is said to develop in the 12 mm. stage(4), when it can be traced forwards to make a connection with the fibres of the posterior commissure which is already well developed. It is also stated(5) that as early as the end of the first month descending fibres from the nucleus of Darkschewitsch can be traced into the posterior longitudinal bundle.

The bundle contains various ascending and descending fibres, and their origin and course is stated somewhat variously by different writers. The most complete summary is that given by Cajal(6). He divides the fibres into an ascending and a descending group with the following components:

(1) *Ascending fibres:*

Arising from (*a*) Deiters' nucleus, many fibres crossed.
(*b*) Substantia gelatinosa Rolando (sensory nucleus of nerve 5).
(*c*) Anterior horn cells of spinal cord.
(*d*) Cells of formatio reticularis.

Ending in (*a*) Nuclei of nerves 6, 4, 3.
(*b*) Interstitial nucleus of Cajal.
(*c*) Posterior commissure.
(*d*) Corpora mammillaria by passing in front of Gudden's tegmental bundle.

(2) *Descending fibres:*

Arising from (*a*) Interstitial nucleus of Cajal.
(*b*) Deiters' nucleus.

Ending in (*a*) Nuclei of nerves 4 and 6.
(*b*) Spinal cord, by anterior ground bundle.

In addition to these fibres, other workers describe the following connections:

(1) *Ascending fibres:*

(*a*) Arising from the superior olive (7).
(*b*) Ending in the nucleus of Darkschewitsch (8, 9, 10).
(*c*) Passing to the optic thalamus (11), the infundibulum and the internal capsule (12).

(2) *Descending fibres:*

(*a*) Arising from the superior olive (7).
(*b*) From the tectobulbar tract at the level of the red nucleus (13).
(*c*) Arising from the ganglion of Gudden (the termination of Gudden's dorsal tegmental bundle at the level of the nucleus of nerve 4) (8).
(*d*) Arising from the nucleus of Darkschewitsch (8, 14, 15).
(*e*) From the posterior commissure, crossed fibres (16).
(*f*) From Gudden's tegmental bundle (faisceau de la calotte de Gudden) (17, 18).
(*g*) Joining emerging fibres of nerves 7 and 12 (19).
(*h*) From the paraventricular (or posterior hypothalamic) nuclei (20).

METHOD

The material on which this paper is based includes serial sections of brain stem from eighteen specimens of the following ages:

*10 mm.	One		22–24 weeks	One
*12 mm.	One		24–26 weeks	One
*17 mm.	One		26–28 weeks	One
20 mm.	One		36 weeks	One
8 weeks	One (unmeasured)		Full time	Two
37 mm.	One	*(One)	3-month infant	Two
10 weeks	One		8-month infant	One
*14–16 weeks	One		9-month infant	One

* Serial, every section.

The younger embryos up to and including the 10-week specimen were fixed whole in formol-saline, cut serially, and the sections stained by Scott's haematoxylin and Biebrich scarlet. The brain stem and in most cases the spinal cord of the older specimens were dissected out, fixed in formalin, and subsequently treated by the Weigert-Pal method. All sections were mounted serially.

The series stained by the Weigert-Pal method is particularly favourable for the study of the development and connections of those tracts that myelinate early, as their paths are not obscured by the general heavy myelination that is present even by 8 months after birth.

OBSERVATIONS

(*a*) **10-*mm. embryo*.** The posterior longitudinal bundle was not identified.

(*b*) **12-*mm. embryo*.** A clearly defined bundle of fibres is present in the floor of the fourth ventricle, on each side of the mid-line, occupying the position in which the posterior longitudinal bundle is found in later stages of development. This group of fibres runs close to the mid-line and parallel with the long axis of the brain stem. It could not be traced higher than the level of the superficial attachment of the fifth cranial nerve.

(*c*) **17-*mm. embryo*.** A bundle of fibres similar to that seen in the 12-mm. embryo was identified, and found extending up to the same level. When traced downwards it was found as a large group of fibres running longitudinally between the olive and the mid-line on each side, and passing anteriorly to take part in the anterior ground bundle in the spinal cord.

(*d*) **20-*mm. embryo*.** Sections through the level of the upper part of the fourth ventricle show well-defined bilateral bundles of fibres just below the floor close to the mid-line. Lower down in the middle pons region the definite bundles are lost, but in the lower pons and medulla regions the fibres are again seen in two discrete fasciculi lying more ventrally.

(*e*) **8-*week embryo*.** The bundle is clearly defined at the level of the nucleus of the fourth nerve. Traced inferiorly the fibres become diffuse, but in the medulla they again make definite fasciculi.

(*f*) **8½-*week embryo* (37 *mm.*).** In this embryo the posterior longitudinal bundle appears as a clearly defined group of fibres extending from about the level of the fourth nerve to the anterior ground bundle in the spinal cord. In the preparations the fasciculus could not be identified at higher levels, but in contradistinction from the younger embryos it formed discrete bundles throughout the pons levels.

(*g*) **10-*week embryo*.** The bundle is considerably larger in size than in the younger embryo. Furthermore it can be traced up into the mid-brain region where it lies in close association with the nuclei of the third nerve and with the red nucleus. At this stage none of the fibres of the tract are myelinated.

(*h*) **14–16-*week foetus*.** This is the youngest specimen stained by the Weigert-Pal method. It shows very slight myelination in the fibres of the bundle, and it may be assumed that no myelination occurs earlier because even at this age the myelin is very scanty and only present in a few of the fibres. Very finely myelinated fibres were traced as far up as the lower end of the third nerve nucleus and as far down as the anterior ground bundle of

the spinal cord. They were most numerous in the medulla, were almost lost in the lower levels of the pons, and again picked up at the upper part of the pons.

The origin of the fibres, although at first difficult to find owing to their small number, was nevertheless quite clear because the fibres of so few tracts show myelination at this age (21). In the medulla myelinated descending fibres arise from Deiters' nucleus and the superior olive in relatively considerable numbers, while ascending fibres arise in the reticular formation cells, but whether any of the fibres arising in Deiters' nucleus and the superior olive were ascending could not be determined. Myelinated connections with the sixth and the fourth nerve nuclei were seen (see diagram 1).

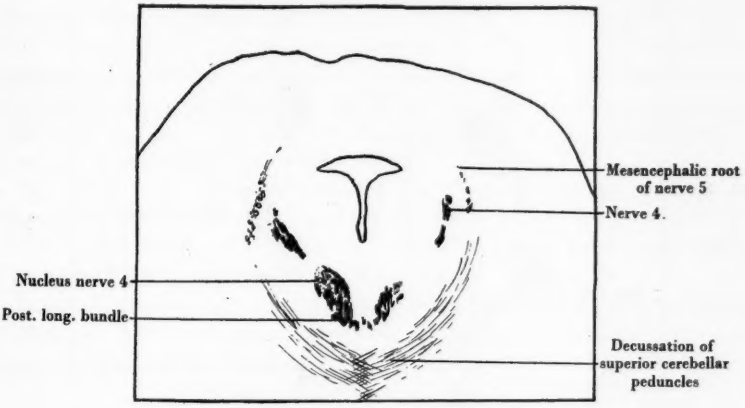

Diagram 1. Foetus 26–28 weeks.

A well-developed nucleus is seen sending a few myelinated fibres towards the posterior commissure, but the posterior longitudinal bundle is not myelinated at this level, so that any possible connection with this nucleus or with the nuclei of the third nerve could not be established. This nucleus is referred to in the remainder of this paper as the nucleus of the posterior commissure or "nucleus 1". In addition a small group of cells was found lying dorso-medial to this nucleus, which is described later as "nucleus 3".

(*i*) **24–26-*week foetus*.** As in the 14–16-week foetus myelination in this bundle is most marked in the medulla. In the lower region of the pons the myelination is less but increases again in the upper pons levels; the whole tract, however, is very much better myelinated than in the younger foetus.

In addition to the connections previously established, myelinated fibres can be seen connecting the bundle with the nucleus of the third nerve, and with the nucleus of the posterior commissure and also connecting this nucleus with the posterior commissure. Myelinated fibres comparable to those which are definitely posterior longitudinal bundle fibres better seen in older specimens

are present running in an oblique direction medial to the red nucleus and connecting at least in part with a small nucleus situated in the floor of the third ventricle in its posterior part (see "nucleus 4" later; see diagram 2). In addition another nucleus composed of large cells (referred to later as "nucleus 2") was found having some myelinated connections with the posterior longitudinal bundle. It is situated ventro-medial to the upper part of the nucleus of the posterior commissure, and rests on the capsule of the red nucleus.

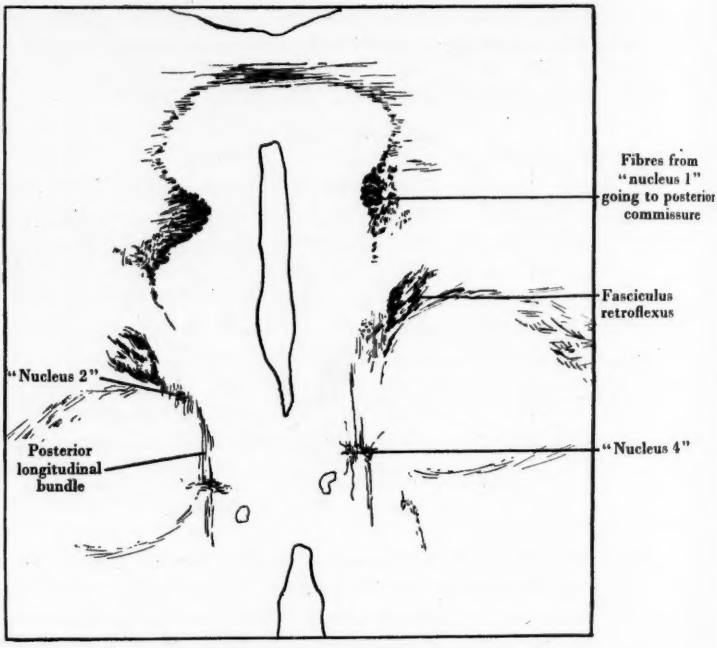

Diagram 2. Full-time foetus. Note "nucleus 4".

(*j*) 26–28-*week foetus*. The only difference noted from specimen (*i*) was the presence of a few fine myelinated fibres of the posterior longitudinal bundle crossing the middle line (see diagram 3) just medial to the point where the fasciculus retroflexus begins to impinge on the capsule of the red nucleus.

(*k*) 36-*week foetus*. No differences were observed from the previous specimen beyond an increase in the number of myelinated fibres in the bundle, and the appearance of myelinated fibres in connection with nucleus 3.

(*l*) *Full-time foetuses* (2 *specimens*). One specimen was better prepared than the other. The crossing fibres of the posterior longitudinal bundle were well marked lying considerably dorsal to the myelinating commissure of Forel,

and in sections showing these commissural fibres other myelinated fibres are seen some connecting probably with the nucleus previously noted in the floor of the third ventricle ("nucleus 4"), and others passing still more ventrally towards the lateral mammillary region. Although no definite connection can be established with the various mammillary nuclei, it is to be noted that fine myelinated fibres are seen in close connection with the cells of the accessory mammillary nucleus.

(*m*) *Three-month infants* (*2 specimens*). The bundle in the upper pons levels, divides into definite fasciculi. The greater degree of general myelination, especially in the higher regions, makes it more difficult to distinguish this bundle from other adjacent fibres. As in the full-time specimens, the fasciculus was traced up to the level of the mammillary region, the myelinated fibres becoming fewer in number and directed obliquely toward the mammillary bodies (see diagram 4). It is very doubtful, however, whether there is any connection with these bodies, and the bundle disappears at the upper level of the red nucleus. The nucleus of the posterior commissure and "nuclei 3 and 4" are well defined, but "nucleus 2" is difficult to identify as it is obscured by the myelinated fibres among which it lies.

(*n*) *Eight-month and nine-month infants.* The observations made on the younger specimens were confirmed in all levels below the nucleus of the posterior commissure. Unfortunately above this level the series of sections is too incomplete to admit of accurate deduction.

It is well known that the appearance of the bundle in section varies considerably at different levels of the brain stem, but as this has been fully described by others (22) it is unnecessary to repeat it here.

DISCUSSION

Examination of this series of specimens confirms the observations of others that the posterior longitudinal bundle appears first in the 12-mm. stage of development.

The fasciculus appears first in the medulla and lower pons levels, and rapidly extends downwards to the cord. The next group of fibres appears in the upper pons level and is not at first connected with the lower fibres, leaving a gap about and above the level of the entry of the fifth nerve. These upper fibres in the 8-week stage extend up to the level of the fourth nerve nucleus, and about the same time or a little later the gap between the first and the second groups of fibres is bridged across, the tract now appearing continuous between the spinal cord and the level of the fourth nerve nucleus. By 10 weeks' development the bundle has almost reached the level of the red nucleus and third nerve nuclei.

Myelination begins in the 14–16-week stage in a few fibres of the bundle. These myelinated fibres are most obvious in the medulla and lowest pons and cord, but almost lost in the lower and middle pons (the region corresponding

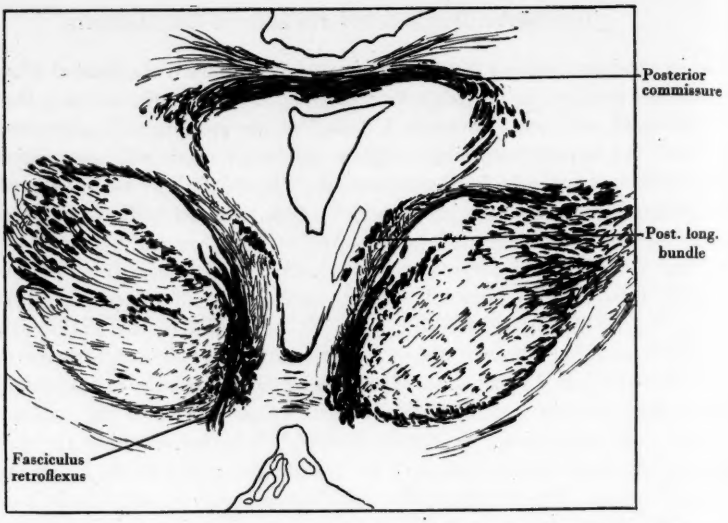

Diagram 3. Infant, 9 months. Note crossing fibres of posterior longitudinal bundle.

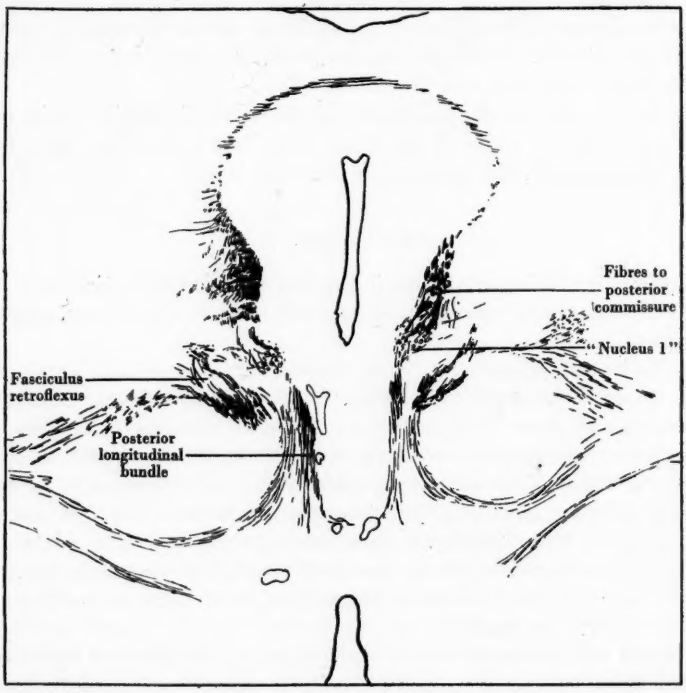

Diagram 4. Full-time foetus.

to the gap that existed during the development of the fibres), and found again through the upper pons up to the lower end of the third nerve nuclei. Myelinated connections with the nuclei of Deiters' and of nerves 6 and 4 are present. Thus myelination occurs first in those fibres that have developed by 8 weeks, and in general myelination in the groups of fibres of the bundle follows in the same order as their development. [It is not suggested that there is any correlation between early development and early myelination; for example, the fasciculus retroflexus and the bundle of Vic D'Azyr are easily distinguished in an 8-week embryo, the former begins to myelinate about 26 weeks, the latter about full-time. The fornix is seen in a 10-week foetus, and myelinates 3 months after birth.]

By 24–26 weeks a myelinated connection is established with the nuclei of the third nerve, the nucleus of the posterior commissure and with "nucleus 2", and about the same time a few myelinated fibres cross near the upper end of the red nucleus just dorsal to the unmyelinated commissure of Forel, and connect with a small ventrally placed nucleus ("nucleus 4"). In the later weeks of foetal life the myelination is increased throughout the bundle, and at full time some fibres can be traced toward the lateral mammillary region.

Thus the component fibres and connections identified in this series correspond with those described by Cajal with the following reservations:

(*a*) Substantia gelatinosa of Rolando. This connection was impossible to identify in the older foetuses owing to the numerous myelinated fibres in the region, but in the 24–26-week specimen it was thought that such a connection existed.

(*b*) Anterior horn cells of spinal cord.

(*c*) Posterior commissure.

(*d*) Corpora mammillaria. No definite connection with these bodies was established.

In respect of connections other than those given by Cajal, the following were established:

(*a*) With the superior olive.

(*b*) With the nucleus of the posterior commissure.

(*c*) With a small ventrally placed nucleus ("nucleus 4").

Furthermore it is suggested that the fibres of the posterior longitudinal bundle crossing in the region of the red nucleus may possibly be those described by Beattie (20) as arising from paraventricular nuclei in connection with the central control of the sympathetic system.

The interstitial nucleus of Cajal and the nucleus of Darkschewitsch

During the study of the connections of the upper end of the posterior longitudinal bundle the authors found that this fasciculus freely connected with a large well-defined nucleus (see diagram 5) which also made abundant connections with the posterior commissure, and has been called, in the earlier

part of the paper (on account of what appeared to be its chief connection), the nucleus of the posterior commissure or "nucleus 1". Judging from its position, and its relation to the posterior commissure, this nucleus should have been the nucleus of Darkschewitsch, for in certain references the terms "nucleus of Darkschewitsch" and "nucleus of posterior commissure" are used synonymously. On the other hand Cajal's diagram shows that his interstitial nucleus (lying nearer the red nucleus) makes more abundant connections with the posterior commissure, than does the nucleus labelled Darkschewitsch; in fact his interstitial nucleus may be said from his diagram to be furnishing the

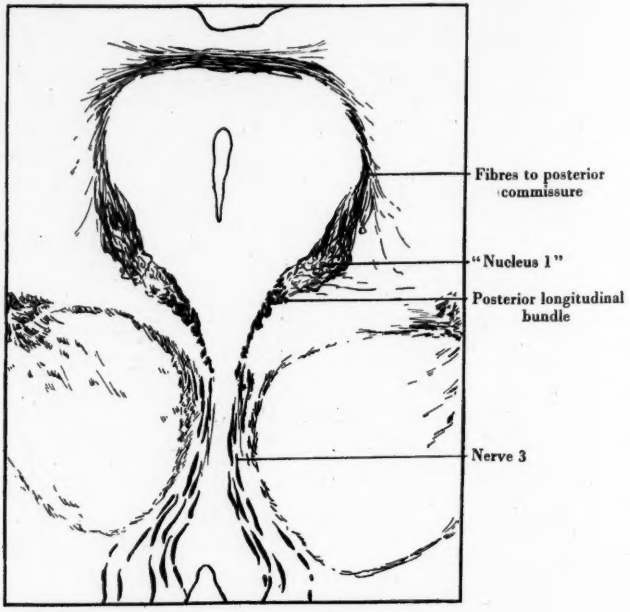

Diagram 5. Infant, 3 months.

bulk of the fibres to the ventral part of the posterior commissure. Search in the older material under investigation for the nucleus lying almost in the capsule of the red nucleus resulted in the establishment of a nucleus consisting of scattered cell groups, intimately related to the posterior longitudinal bundle but with no very apparent connection with the posterior commissure. This nucleus consisting in the older specimens of scattered cells was identified with a much more definite and discrete nucleus in the 24–26-week foetus and was called "nucleus 2" (see diagram 6). Two other nuclei had also been observed having connections with the posterior longitudinal bundle. The difficulty then arose as to which of these nuclei corresponded to the interstitial nucleus of

Cajal, and to the nucleus of Darkschewitsch. A careful review of the literature on the subject of these nuclei was accordingly made. It was found that the descriptions by the various authors showed great discrepancies, not to say confusion (see Cajal (6), Gray (19, 24), Foix (25, 27), Ranson (23), Poirier and Charpey (28), van Gehuchten (26) and Winkler (14)).

A further careful study of the cells of this region was accordingly made in the material under investigation: the following account summarises the cell masses found in connection with the posterior longitudinal bundle, and the four nuclei which were found are carefully described as to position and connections, but in order to avoid further confusion in nomenclature they are referred to by numbers and the names used by Darkschewitsch and Cajal have been omitted.

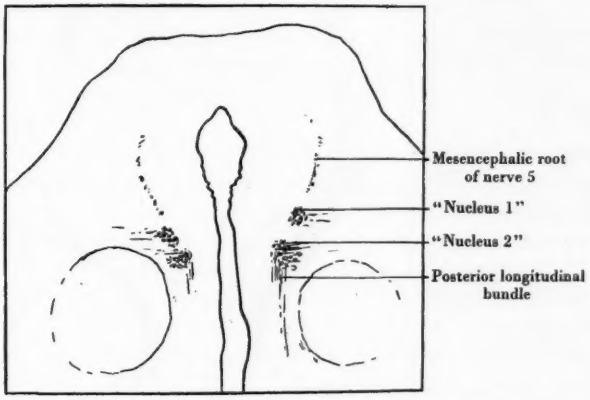

Diagram 6. Foetus of 24–26 weeks. [The red nucleus has been outlined, but no myelinated fibres are present in its capsule.]

Nucleus 1 (diagram 5), referred to in the previous part of this paper as the nucleus of the posterior commissure. This nucleus has its most bulky connection with the ventral part of the posterior commissure, and these fibres begin to myelinate as early as 14–16 weeks (i.e. before myelination of the posterior longitudinal bundle in this region). Myelinated connections between this nucleus and the posterior longitudinal bundle occur later, and furthermore myelinated fibres pass out laterally from this nucleus towards the thalamus (external nucleus) and also in the radiations of the calotte towards the globus pallidus. This nucleus is situated on the edge of the central grey matter surrounding the Sylvian aqueduct, and extends from the middle part of the third nerve nuclei up to the opening of the aqueduct into the third ventricle, that is to the level at which the fasciculus retroflexus is entering the capsule of the red nucleus.

Nucleus 2 (diagram 6). This nucleus appears in the higher sections of midbrain in which "nucleus 1" is disappearing. It lies slightly medial and ventral

to "nucleus 1", resting on the capsule of the red nucleus, and between this nucleus and the myelinated fibres of the posterior longitudinal bundle, with which it appears to be connected. It consists of cells scattered in groups, and in older specimens it tends to become obscured by the increase of myelinated fibres in this region. It extends upwards to the upper limit of the posterior longitudinal bundle, that is to the upper end of the red nucleus. The nucleus was identified in the 14–16-week foetus, but not looked for earlier. Connections with the posterior commissure, if present, were difficult to establish.

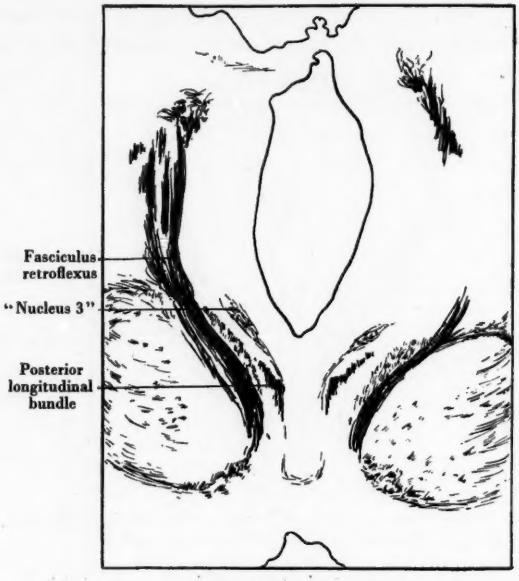

Diagram 7. Infant, 3 months. Note fine fibres passing ventrally from "nucleus 3".

Nucleus 3. This nucleus in the 3-month infant is well defined, and lies just within the lateral margin of the central grey matter of the floor of the Sylvian aqueduct (see diagram 7). Caudally it is found dorso-medial to "nucleus 1", and maintaining the same situation in the mid-brain it extends upwards to near the upper extremity of the red nucleus. A group of cells in a corresponding position was seen in the 14–16-week foetus but was not identified in sections of foetuses between this age and 36 weeks, by which stage a definite nucleus was seen with a few fine myelinated connections running in the direction of the posterior commissure. At birth this nucleus was definitely connected with fine myelinated fibres which pass ventrally medial to the posterior longitudinal bundle, some of these fibres crossing in the dorsal part of the commissure of Forel.

Nucleus 4 (diagram 2). This is a very small nucleus present in all specimens older than 26 weeks lying in the floor of the third ventricle, medial to the red nucleus. It connects at least in part with the fibres of the posterior longitudinal bundle which in these sections are seen running in an oblique direction medial to the red nucleus. The myelinated fibres connected with this nucleus present a very characteristic appearance, because in addition to the fibres of the posterior longitudinal bundle running in a dorsi-ventral plane, there are other fibres (of unidentified destination) in connection with the nucleus which run medially and horizontally.

Cajal's description of the interstitial nucleus agrees with regard to its position with "nucleus 2" of this paper, but in the human foetus we did not find it abundantly connected with the posterior commissure as his diagrams of the nuclei in the cat suggest.

"Nucleus 1" in our material was the one most profusely connected with the posterior commissure: many writers speak of Darkschewitsch's nucleus as synonymous with that of the posterior commissure, and we feel that this name best describes it.

"Nucleus 3" on account of its position might be called the nucleus of Darkschewitsch because it lies just within the central grey matter, and though its earliest myelinated connections are with the posterior commissure, they are very scanty. Its later and more profuse connections are in a ventro-medial direction. Its fibres differ from those of "nucleus 1" in that they are much finer, and throughout our series it appears as a definite and discrete nucleus; furthermore it was seen in the highest sections that also show "nucleus 1", and when "nucleus 1" disappears it was present in sections showing "nucleus 2".

"Nucleus 4" does not seem to have been described previously unless it is the "interstitial nucleus" described in Gray's text-book of *Anatomy* (19) as "a small collection of cells situated in the lateral wall of the third ventricle immediately above the upper end of the cerebral aqueduct." It is in any case very small in comparison with the other nuclei of the posterior longitudinal bundle.

The authors feel that "nucleus 1" may well be described as the *nucleus of the posterior commissure*, and "nucleus 2", since it lies among the fibres of the posterior longitudinal bundle, as the *interstitial nucleus of the posterior longitudinal bundle*.

SUMMARY

1. The posterior longitudinal bundle appears first in the 12-mm. embryo.

2. This bundle is one of the earliest to myelinate, the process beginning at about 14 weeks.

3. In the early weeks of development (previous to $8\frac{1}{2}$ weeks) there are two unconnected groups of fibres:

(*a*) A group connected with Deiters' nucleus which extends up into the lower pons, and downwards into the medulla and spinal cord.

(*b*) A group found in the upper pons region extending up to the fourth nerve nucleus.

4. At 14 weeks myelinated connections of the bundle are seen with the nuclei of Deiters' and of the sixth and the fourth nerves.

5. At 24 weeks myelinated connections occur with the nuclei of the third nerve and of the posterior commissure ("nucleus 1").

6. The various groups of fibres of the bundle myelinate in the same order as that in which they developed.

7. Myelinated fibres are seen within "nucleus 2" about 24–26 weeks: these may or may not at this age connect with the posterior longitudinal bundle.

8. Definite myelinated connections between the posterior longitudinal bundle and "nucleus 4" are seen at 26–28 weeks.

9. Myelinated connections of "nucleus 3" are seen at 36 weeks.

10. About 28 weeks a few myelinated fibres are seen crossing the mid-line in the supra-mammillary region their destination (or origin) is uncertain and they continue to increase in numbers in the older specimens, though all do not cross.

11. The nucleus of the posterior commissure ("nucleus 1") makes a definite connection with the posterior longitudinal bundle, and furnishes a large contingent of fibres to the ventral part of the posterior commissure.

12. In the region of the nuclei described by Darkschewitsch and Cajal four nuclei have been identified and described.

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* When this paper was ready for the press we received a note from Professor S. W. Ranson (Chicago) saying that he also has been investigating the nucleus of Darkschewitsch and the interstitial nucleus of Cajal, and was shortly publishing a note on their topography.

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THE MEDIAL GENICULATE BODY AND THE NUCLEUS ISTHMI

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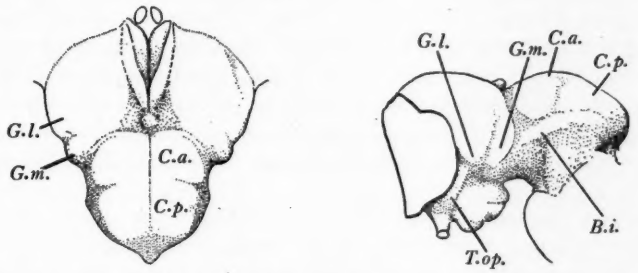
In the small brains of primitive Mammals such as insectivores, the medial geniculate body forms a conspicuous rounded tubercle projecting from the lateral aspect of the caudal end of the thalamus. Topographically it appears to be essentially a part of the latter, for while it is marked off from the mid-brain by a relatively deep furrow, it is separated from other thalamic elements such as the lateral geniculate body and the pars posterior of the lateral nucleus (pulvinar) superficially by quite shallow grooves. It is held by many authorities, however, on the basis of comparative anatomical studies, that the medial geniculate body is rather to be regarded as a mesencephalic element which has become secondarily approximated to the diencephalon during the course of evolutionary differentiation of the fore-brain, and it is one of the aims of this paper to consider this interpretation.

Coronal sections through the medial geniculate body of insectivores (e.g. *Erinaceus* and *Sorex*) show that in its cyto-architecture it consists mainly of a homogeneous group of rounded and fairly large polygonal cells of uniform size which are scattered evenly throughout the nucleus. This may be called the principal nucleus of the medial geniculate body. It marks the termination of the bulk of the fibres forming the brachium inferius of the posterior colliculus and it gives off contributions to the thalamic radiations which at first pass forwards medio-ventral to the optic radiations emerging from the lateral geniculate body, and then turn laterally to reach the cortex. There is experimental evidence to indicate that these cortical connections conduct in both directions and are essentially related to the area temporalis of the neopallium.

If coronal sections of the insectivore brain are traced rostrally, the principal nucleus of the medial geniculate body is found to pass without any demarcation or interruption directly into the ventral nucleus of the thalamus, which is made up of precisely the same type of cell. This broad continuity of the medial geniculate body with the ventral nucleus is well shown in horizontal sections through the diencephalon of *Sorex*. In this primitive brain, therefore, the geniculate body is merely the latero-caudal part of the main sensory nucleus of the thalamus, and is not to be distinguished from the latter except by its topographical position and its fibre connections (especially with the inferior brachium). In the brains of larger Mammals the medial geniculate body undergoes a caudal displacement consequent mainly upon the expansion of the lateral

nucleus of the thalamus. A study of a graded series shows that in this way it becomes extruded caudo-ventrally and finally "pinched off" from the main part of the ventral nucleus, and its connection with the latter thus becomes increasingly indistinct. Nevertheless, such a connection has been noted in higher mammalian brains. Thus Rioch (20), and later Ingram, Hannett and Ranson (9), note a continuity between the medial geniculate body of Carnivora and the pars arcuata of the ventral nucleus, and Papez (16) has recently indicated a similar relation in the armadillo.

The common origin of the principal nucleus of the medial geniculate body and the ventral nucleus of the thalamus is indicated clearly enough in the brain of the human embryo. Thus, Plate I, fig. 1 represents a horizontal section through the diencephalon and mid-brain of a human embryo of 92 mm. C.-R. length, in which the cells of the medial geniculate body merge with those of the ventral thalamic nucleus to form a common mass which extends caudo-



Text-fig. 1. Dorsal and lateral views of the diencephalon and mid-brain of a 92 mm. human embryo. × 3.

B.i. inferior brachium. *C.a.* anterior colliculus. *C.p.* posterior colliculus. *G.l.* latera geniculate body. *G.m.* medial geniculate body. *T.op.* optic tract.

laterally to the surface of the thalamus. It may be noted, further, that the superficial cells of both lateral and medial geniculate bodies form a continuous stratum although the former (which is also derived from the common ventral nuclear mass) is otherwise well defined at this stage of development by medullary laminae. In the section, fibres of the brachium inferius can be seen entering the caudal extremity of the medial geniculate body. The dorsal and lateral aspects of the diencephalon and mid-brain of the embryo from which this section was taken are illustrated in text-fig. 1. From this, it will be seen that in the 92 mm. stage the two geniculate bodies occupy the primitive position which is found in Insectivora, that is to say, they form low elevations on the lateral wall of the thalamus proper and are not yet overhung by a caudally projecting pulvinar. The medial geniculate body occupies a rostral position relative to the mid-brain, and passing forwards and downwards to it on the lateral aspect of the latter is to be seen very distinctly a broad white band, the inferior brachium.

Ventral to the principal nucleus of the medial geniculate body in the insectivore brain and extending to its caudal margin is a flattened plate of spindle-shaped cells which may be called the ventral nucleus of the medial geniculate body. It runs into direct continuity medially with the zona incerta of the subthalamus, and rostrally it is continuous with the nucleus reticularis thalami (which, incidentally, should not be included among the nuclei of the thalamus proper for it is nothing more than an extension dorso-laterally of the subthalamus to form a thin shell covering the lateral surface of the thalamus and penetrated everywhere by the thalamic radiations). It represents the *noyau suspédonculaire* of Cajal (1) in the mouse brain, the *noyau caudal gris* of Vogt (27) in the medial geniculate body of *Cercopithecus*, the caudo-ventral element of Friedemann (5), Pines (17), and Clark (2) in *Cercopithecus*, *Lemur*, and *Tarsius* respectively, the *nucleus infrageniculatus* of Přechechtěl (19) in the elephant, the *c* nucleus of Winkler and Potter (25, 26) in the rabbit and cat (in which these authors note it is united with the ventral part of the formatio reticularis), and the marginal nucleus of Winkler (24). It is with the ventral nucleus of the medial geniculate body that the commissure of Gudden appears to be principally related. Winkler states that after removal of the hemisphere in the rabbit, while the main part of the medial geniculate body undergoes complete atrophy, this is not the case with his marginal nucleus. Meyjes (14) found no degeneration in the *c* nucleus after lesions involving the area temporalis of the cortex in the rabbit.

By Rioch (in carnivores) and Papez (in *Tatusia*), this element is not distinguished from the reticular nucleus. It should, however, be included in the medial geniculate body, for in many Mammals it becomes incorporated with the principal nucleus (and intimately related to it) in the eminence of the medial geniculate body. Its connections with the zona incerta become much less obtrusive in the brains of higher types (in association with the displacement of the body ventro-caudally in these forms), and sagittal Weigert sections in *Erinaceus* and *Tarsius* show that it receives a contribution from the inferior brachium. In these animals, also, the ventral nucleus of the medial geniculate body is connected with the subthalamus by fine myelinated fibres (see text-fig. 2), the ultimate destination of which cannot be determined by normal Weigert material.

Thus the medial geniculate body in its simplest form is found from a study of mammalian brains to consist essentially of two diencephalic elements which are differentiated respectively from the ventral nucleus of the thalamus proper and the subthalamus. These divisions are, moreover, directly comparable with the two elements of the lateral geniculate body. The dorsal nucleus of the latter (corresponding to the nucleus principalis of the medial geniculate body) is delaminated off from the lateral aspect of the main sensory nucleus of the thalamus in association with its optic connections (4) and gives off cortical projection fibres, while its ventral nucleus I have shown (3) to be really a differentiated lateral portion of the subthalamus (which was confirmed later by

Papez (16). There is no evidence in the mammalian series of a phylogenetic shifting forwards of the medial geniculate body relative to the mid-brain. Gurdjian's statement (6) that in the rat's brain the body is situated more caudally than in the brain of higher Mammals rests on an error of interpretation related to the fact that in the rat there is no caudally projecting pulvinar.

The relation of the medial geniculate body to other nuclear elements in the caudal part of the thalamus, especially the pars posterior of the lateral nucleus (pulvinar), requires emphasis. It has been pointed out in previous papers (2, 4) that in primitive mammalian brains the pars posterior of the lateral nucleus extends back in a caudo-ventral direction and that its caudal extremity intervenes between the medial geniculate body ventro-laterally and the pretectal nucleus dorso-medially. It appears that this caudal extremity has been described by some authorities as an integral part of the medial geniculate body. Cajal (1) described dorsal and ventral lobes in the medial geniculate body of the mouse. The ventral lobe is the principal termination of the lateral lemniscus and gives off auditory radiations, and it evidently corresponds to the principal nucleus as described above. On the other hand, the afferent connections of the dorsal lobe are uncertain, though Cajal thinks they may be derived from the posterior colliculus. Further, Cajal quotes von Monakow to the effect that while ablation of the auditory cortical area in Mammals is followed by atrophy of the ventral lobe, the superior lobe remains unaffected. Cajal's figures (which I have compared with serial sections through a mouse brain) confirm the supposition that, in its topographical position, and especially in its relation to the lateral geniculate body and the optic tract, his superior lobe is really the caudal end of the pars posterior of the lateral nucleus. In 1902, Munzer and Wiener mistook this element for the medial geniculate body in the rabbit (as, indeed, has already been pointed out by Rioch), and the same interpretation applies to the dorsal nucleus of the medial geniculate body of Winkler, or the *b* nucleus of Winkler and Potter in the rabbit. Yoshida (28) found that after lesions involving the cortex of the temporal lobe in the rabbit, cell degeneration was practically confined to his ventral nucleus of the medial geniculate body. On the other hand, the dorsal nucleus was intact except for its extreme medio-ventral angle where there was also some cytolysis, and it seems probable that this atrophy was due to the slight involvement of the cortex immediately adjacent to the area temporalis superior. In a recent and admirable monograph by Posthumus Meyjes (14), a similar error in identification is made. The excellent photographs in this paper show that the *b* nucleus of this author is a direct extension of the pulvinar, being covered by the main mesencephalic root of the optic tract and penetrated by many of its fibres, while the cell group which lies on the tectal side of the nucleus limitans and which recent studies of the mammalian thalamus have shown to be the nucleus pretectalis, has been labelled the pulvinar. Meyjes applies the term nucleus suprageniculatus to the caudal extremity of his nucleus *b*, but, again judging from his figures, it seems certain that his nucleus profundus represents the nucleus suprageniculatus as it has

been defined in recent literature. This author found only a simple general atrophy of the medial geniculate body in rabbits after cortical lesions involving the temporal areas, without the cell loss and gliosis which is exhibited in the lateral geniculate body after lesions of the visual cortex. According to his account, the general appearance of the medial geniculate body was normal in these experiments, and the simple atrophy could only be recognised by careful comparison with the normal side. This was not the experience of Yoshida who states that, after similar cortical lesions "sind die meisten Zellen schon verschwunden, und die Gliawucherung ist sehr deutlich." The results of Meyjes' first series of experiments are difficult to assess, partly because the cortical lesion was only in one case limited to the area temporalis proper, and partly because the staining method which he used (Weigert-Pal and van Gieson) is not very suitable for determining the precise origin of fibres which had been involved by the experiment. In the case in which the lesion was limited to the area temporalis, it is observed that while very little difference was found between the geniculate bodies of the two sides, there was a slight indication of a simple atrophy affecting mainly the *a* nucleus (i.e. the nucleus principalis of the present description) of the operated side. The Marchi experiments of this author, however, demonstrated that degeneration in the *b* nucleus only occurred after lesions which were situated at the upper corner of the area temporalis, i.e. which involved to some extent the immediately adjacent visual cortex.

It appears, therefore, that, on the basis of cortical connections, there is no convincing experimental evidence for the inclusion of the pars posterior of the lateral nucleus (nucleus *b*) as an integral element of the medial geniculate body. It may be further noted, also, that there is no evidence that this element receives lateral fillet fibres or is in direct relation with the brachium inferius.

Apart from these misinterpretations, however, there is evidence that in higher mammalian forms, the lateral thalamic nucleus does contribute an element which becomes incorporated in the structure and the eminence of the medial geniculate body. In *Tarsius* (2) the dorsal and lateral surfaces of the body are formed by a layer of cells rather larger and more deeply stained than those in the central part, and this element has been termed the pars lateralis. It is found to be directly continuous rostrally with the nucleus suprageniculatus which, appearing as a condensation of the cells of the caudal end of nucleus lateralis *b* of the thalamus near the dorsal surface of the latter, extends downwards, backwards and outwards to reach the medial geniculate body. Text-fig. 2 represents a sagittal section of the medial geniculate body of *Tarsius* at the level of which the nucleus suprageniculatus becomes incorporated in its dorsal part. It will be observed that the nucleus does not appear to be related terminally with the inferior brachium. On the other hand, it emits cortical fibres which pass forwards to the internal capsule immediately dorsal to the auditory radiations emerging from the central part (nucleus principalis) of the medial geniculate body. This disposition of the nucleus suprageniculatus, which is so diagrammatically clear in the simple brain of *Tarsius*, becomes consider-

ably obscured in higher Primates. The line of demarcation between the medial geniculate body and the pulvinar also becomes less clear in Nissl preparations in association with the development of rich internuclear connections which tend to break up the outlines of these two elements where they come into contact. Friedemann (5) describes and figures a lateral large-celled element in the medial geniculate body of *Cercopithecus* which is similar to the pars lateralis of *Tarsius*. In the monkey, however, its direct connection with the lateral nucleus of the thalamus seems to be broken and represented by more or less isolated groups of cells in the nucleus limitans and especially the pars supragenicula ta nuclei limitantis. The nucleus limitans of the higher Primates is probably a composite structure into which several distinct thalamic elements enter. Its elementary composition is shown clearly in fig. 8 of my paper on the thalamus of *Tarsius*, and a comparison of this with the figures of Friedemann (*Cercopithecus*) and Pines (*Lemur*) shows that in the higher Primates it is formed by a compressed lamina of cells involving from above downwards the large-celled nucleus of the optic tract, the nucleus suprageniculatus, and the nucleus parafascicularis. Rioch describes in Carnivora a direct connection between a part of the medial geniculate body and the nucleus suprageniculatus, and this is confirmed by Ingram, Hannett and Ranson. It should be noted, however, that in its intrinsic structure, the topographical disposition and cyto-architecture of the nuclear elements of the medial geniculate body in this specialised mammalian group do not appear to be directly comparable with those found in the Primates.

Another element has been described by Vogt, Friedemann, and Pines, under the name of the *noyau basal* or nucleus parageniculatus, which is topographically closely related to the medial geniculate body in the monkey and lemur. These authors regard it as equivalent to the nucleus parageniculatus of Lewandowsky and as a part of von Monakow's nucleus ventralis *c*. Possibly, also, it may correspond to the corpus geniculatum mediale accessorium of Marburg in the human thalamus. The significance of this element still remains obscure, but it seems fairly clear that it cannot be regarded as a part of the medial geniculate body.

THE NUCLEUS ISTHMI

In the reptilian brain, there is a conspicuous group of cells which bears an intimate relation to the lateral fillet called the nucleus (or ganglion) isthmi. It is commonly held by those observers who have made a study of this nucleus that it is the reptilian homologue of the medial geniculate body in Mammals. Joustra's study (10) of the nucleus isthmi in the crocodile and chameleon led him to this conclusion and, three years later, Kappers and Fortuyn, in their classical treatise on the comparative anatomy of the nervous system (11), reviewed the evidence in great detail. They note that in many Reptiles the nucleus forms a macroscopic swelling and lies at the edge of the anterior medullary velum immediately in front of the superficial origin of the trochlear nerve. They describe connections of the nucleus with the lateral fillet, tectum, corpus

posticum (which is probably the equivalent of the posterior colliculus), and probably with the commissure of Gudden (commissura transversa, dorsal part of the ventral supra-optic decussation). The nucleus isthmi in the frog was described in detail by Larsell (13) who first distinguished clearly between this nucleus and the secondary visceral nucleus of Fishes and Amphibia (with which the nucleus isthmi had been confused by some earlier writers). Larsell records that the nucleus isthmi is a mesencephalic element and receives fibres from the lateral lemniscus which accompanies the spino-tectal tract on its way to the tectum. He found also the following connections: tractus tecto-isthmi, tractus quadrigemino-isthmialis (from the posterior colliculus), tractus isthmio-tectalis (ending in the deeper layers of the tectal cortex), tractus isthmio-thalamicus, commissural fibres running through the anterior medullary velum, and commissural fibres forming Gudden's commissure. Huber and Crosby (8) found similar connections in the alligator (but do not mention an isthmio-thalamic tract). They state that the fibres of the lateral fillet end mostly in the posterior colliculus, a smaller number terminating in the optic tectum and the nucleus isthmi, and they mention groups of cells intermingled with the fibres of this bundle which they regard as the nucleus of the lateral lemniscus. Shanklin (22) deals with the nucleus isthmi in the chameleon in which it is unusually large, bulging over the superficial origin of the fourth nerve. Besides many of the connections already noted, he describes a connection with the nucleus profundus mesencephali and also figures a tract running from the nucleus to the trochlear nucleus and the posterior longitudinal bundle. In *Sphenodon*, Hindenach (7) describes a dorso-lateral pars magnocellularis of the nucleus isthmi, and a medio-ventral pars parvicellularis. The nucleus is crossed dorsally by the trochlear nerve and is separated medially from the posterior colliculus by the mesencephalic tract of the fifth nerve. It receives caudally fibres from the lateral lemniscus and is connected with the optic tectum and posterior colliculus, as well as with the opposite nucleus by commissural fibres crossing in the anterior medullary velum. Ventral to it is a flattened nucleus lying in the stream of the lateral lemniscus which is called the nucleus of the lateral lemniscus.

It will be apparent that there are very serious objections to the common conception that the nucleus isthmi of the reptilian brain is homologous with the medial geniculate body of Mammals. The former is without doubt a mesencephalic element, situated indeed in the caudal region of the mid-brain, while the principal nucleus of the medial geniculate body—as has been shown above—is just as clearly a diencephalic element derived from the main sensory nucleus of the diencephalon. Further, the relation of these two structures to the lateral fillet is different, for in Reptiles the nucleus isthmi lies in the course of this tract on its way up to the roof of the mid-brain. Kappers has pointed out that it would be surprising if an element such as the nucleus isthmi, which is so constantly to be found in the reptilian brain, were not also represented in Mammals. If it is so represented, however, it is most likely to be found in

relation to the lateral fillet in the region where this tract is running to its main termination in the nucleus of the posterior colliculus.

In Plate I, fig. 3 is shown a photograph of a coronal section through the mid-brain of *Lacerta viridis* at the level of the nucleus isthmi, stained by the Weigert-Pal method and counter-stained with neutral red. In Plate I, fig. 4 is shown a section through the mid-brain of the primitive insectivore *Macroscelides*, stained by the same method. A comparison of these two specimens is instructive. In the lizard, the nucleus isthmi stands out as a group of intensely stained cells lying at the ventro-lateral margin of the tectum close to the trochlear nerve and related medially to a stream of the lateral lemniscus fibres which are passing dorso-medially towards the posterior colliculus. In *Macroscelides*, a conspicuous group of closely packed cells with similar staining properties is seen in a corresponding position lying immediately ventral to the cross-section of the caudal end of the brachium inferius and related in the same way to the fourth nerve and the fibres of the lateral lemniscus system. This nucleus has been variously labelled by other authors as the dorsal nucleus of the lateral lemniscus, the parabigeminal nucleus, and the nucleus bigeminalis (*vide infra*). Here, for reasons which will be advanced, it is termed the nucleus isthmi.

The lateral fillet in *Macroscelides* forms a broad and dense fasciculus running up on the lateral surface of the mid-brain. In the ventral part of its course it encloses an elongated strip of grey matter formed of small and somewhat scattered cells, which is evidently the ventral nucleus of the lateral fillet. More dorsally, the main part of the lemniscus runs straight on into the nucleus of the posterior colliculus, but where it comes into relation with the deep aspect of the nucleus isthmi it appears to contribute some fibres which end here. Thus it seems certain that the nucleus isthmi in this insectivore receives afferent fibres from the octavus system. It has been established (de Lange (12), Winkler (24), Poliak (18)) that the most superficial fibres of the lateral fillet system are tectopontine fibres which degenerate after lesions involving the posterior colliculus and which pass down to the nucleus lateralis pontis. This component of the lateral fillet can be recognised in the *Macroscelides* material and a large proportion of its fibres appear to take origin in the nucleus isthmi. They are more finely medullated than the main part of the fillet and can be traced down in a circumscribed bundle to the lateral nucleus of the pons. Diffuse fibre connections are also to be seen linking the nucleus isthmi with the posterior colliculus, and running medially towards the mid-line where they enter the posterior longitudinal bundle, or cross to the opposite side as the commissure of Probst.

The nucleus which has thus been briefly described in *Macroscelides* is also quite as obtrusive in the brains of *Tupaia*, *Microcebus*, and *Tarsius*, but much less conspicuous in the brains of such insectivores as *Erinaceus* and *Sorex*. In the former examples the tectum is relatively large, while in the latter it is much reduced. There appears, in fact, to be a relation between the size of the tectum and the degree of development of the nucleus isthmi in Mammals. This corre-

sponds with the fact that in Reptiles, in which the tectum is a highly elaborate structure, the nucleus isthmi is particularly well differentiated. In *Erinaceus* and *Sorex*, the nucleus is continuous with little interruption with the cells loosely scattered among the fibres of the dorsal part of the main portion of the lateral lemniscus. This relationship leads to the supposition that the nucleus isthmi is but a differentiated part of the dorsal nucleus of the lateral lemniscus, which has been frequently described in the mammalian brain. It is in the primitive *Tarsius* that the nucleus isthmi is best developed, and as there are available to me series of sections of this brain cut in three planes, I have used this material for making a more complete study of it.

If the lateral aspect of the mid-brain of *Tarsius* is examined macroscopically, the nucleus isthmi is quite apparent as an oval grey eminence 1·5 mm. in length lying over the lateral fillet immediately behind the caudal end of the inferior brachium and in close relation with the superficial origin of the trochlear nerve (Plate I, fig. 2). In Nissl preparations, this tubercle is found to consist of a clearly circumscribed nucleus of closely packed cells, triangular and polygonal in shape and of medium size. It is in immediate relation with the main part of the lateral fillet the lateral fibres of which separate it from the diffusely scattered cells which stream in linear arrangement along the course of the fillet and which constitute the nucleus proper of the lateral lemniscus. Weigert preparations demonstrate the connections of the nucleus isthmi very clearly. In *Tarsius* the octavus system is highly developed, and the whole course of the lateral fillet stands out with unusual distinctness. In text-fig. 2 is shown a sagittal section taken through the lateral part of the diencephalon and which cuts through the elevated tubercle of the nucleus isthmi. Here the nucleus is seen to be in direct connection with the caudo-ventral fibres of the inferior brachium through which it is brought into fibre relation with the medial geniculate body. In its posterior margin is seen the termination of the most rostral and lateral fibres of the lateral lemniscus system. These fibres can be traced ventrally in the more medial sections of this sagittal series, and while some of them—from the deeper part of the nucleus—are undoubtedly derived from the trapezoid system (the bulk of which passes up behind the nucleus isthmi to the posterior colliculus), the majority are related below to the nucleus lateralis pontis and thus form a part of the tecto-pontine system. These sections also demonstrate a fibre connection between the deep aspect of the nucleus isthmi and the posterior colliculus.

In text-fig. 3 is shown a section—taken from a horizontal series of Weigert preparations—through the diencephalon and mid-brain of *Tarsius*. The prominence of the nucleus isthmi is well shown here, as well as its close topographical relation to the superficial origin of the trochlear nerve. The nucleus is partly encapsuled by the most anterior fibres of the lateral lemniscus system and is richly permeated by a fine network of medullated fibres derived from this. Fine fibres can also be seen coursing directly medially from the nucleus into the tegmental part of the mid-brain. This section displays particularly well the

course of the fibres of Gudden's commissure. The more lateral of these fibres penetrate the rostral margin of the medial geniculate body. The medial fibres, however, form a fine stream which runs back medial to the ventral part of the geniculate body and which can be traced caudally as far as the nucleus isthmi. There is little doubt that these fibres have a direct relation with the nucleus.

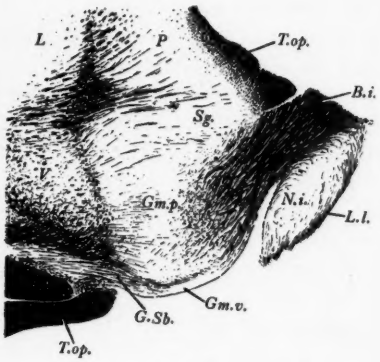


Fig. 2.

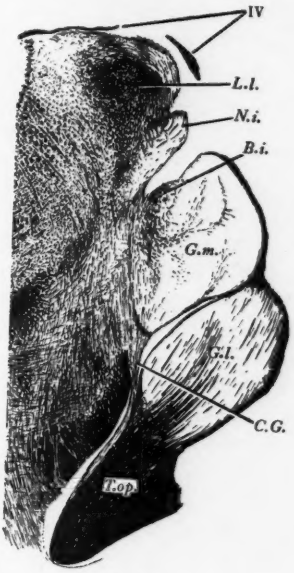


Fig. 3.

Text-fig. 2. Sagittal section through the medial geniculate body and nucleus isthmi of *Tarsius*. Weigert-Pal. ×14.

B.i. inferior brachium. *Gm.p.* principal nucleus of medial geniculate body. *Gm.v.* ventral nucleus of medial geniculate body. *G.sb.* geniculo-subthalamic tract. *L.* lateral nucleus of thalamus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *P.* pulvinar. *Sg.* nucleus supragenicu-latus. *T.op.* optic tract. *V.* ventral nucleus of thalamus.

Text-fig. 3. Horizontal section through the diencephalon and mid-brain of *Tarsius*. Weigert-Pal. ×12.

B.i. inferior brachium. *C.G.* commissure of Gudden. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *T.op.* optic tract. *IV*, trochlear nerve.

Coronal sections of the *Tarsius* brain show similar fibre relations. Here, again, the most rostral fibres of the lateral fillet system are linked up with the medullary plexus which pervades the nucleus isthmi and partly enclose the latter to form a medullary capsule. Following the sections caudally, it appears that many of these fibres form a part of the tecto-pontine system, while at least a proportion of them are derived from the main part of the lateral lemnis-cus which is continued up from the trapezoid body. Some fibres are also seen

running medially from the nucleus isthmi and disappear in the tegmental region of the mid-brain, and there is a connection by diffuse fibres running dorso-medially with the deep strata of the anterior colliculus.

A survey of the literature shows that in many mammalian brains the nucleus isthmi as here defined has been included under the term nucleus dorsalis lemnisci lateralis. Winkler and Potter have thus figured it in their atlases of the cat and rabbit brain, and note that it is characterised by large cells. Winkler states that this dorsal nucleus of the lateral lemniscus receives a large proportion of the fibres of the lateral part of the lateral fillet, which are derived from the superior olivary nuclei through the trapezoid system. Unilateral extirpation of the tuberculum acousticum and the ventral cochlear nucleus in the rabbit leads to some atrophy of the nucleus, and after a superficial lesion in the posterior colliculus Marchi degeneration demonstrates that some of the tecto-pontine and tecto-reticular fibres end in it. It is held that the nucleus transmits impulses to the motor nuclei in the brain stem by way of the posterior longitudinal bundle and the fasciculus praedorsalis. Stokes (23) also describes in the opossum connections from the nucleus of the lateral fillet to the posterior longitudinal bundle, some of which are believed to decussate (Probst's commissure).

The nucleus isthmi of the mammalian brain which has been described in this paper is evidently a differentiated portion of what has usually been called the dorsal nucleus of the lateral fillet. In its topographical position relative to the lateral fillet, the posterior colliculus, and the superficial origin of the trochlear nerve, in the staining properties of its cells, and in its fibre connections with the lateral fillet, posterior colliculus, optic tectum, and Gudden's commissure, this nucleus is clearly the homologue of the nucleus isthmi of reptiles. In a private communication, Prof. Ariëns Kappers has informed me that, following Přechechtěl's observations on the structure of the elephant's brain (19), he is now of opinion that the magnocellular element of the ganglion isthmi of sub-mammalian forms is represented in Mammals by the nucleus lemnisci lateralis dorsalis. Přechechtěl notes that this nucleus occupies a position which corresponds with the ganglion isthmi of Reptiles, but he believes also that the medial geniculate body may represent the chief part of the ganglion isthmi of lower vertebrates, "having shifted in a frontal direction." Papez (15) briefly mentions the nucleus isthmi in a macroscopical description of the dog's brain, and also figures it in the cat's brain. He calls it the nucleus bigeminus, but this term should be discarded, since it has previously been employed by Kappers for quite a different element in the hind-brain. Papez records a bigemino-pontine tract of fibres arising from the nucleus, and as he uses the same name for a tract passing from the nucleus isthmi of birds to the region of the pons, he implies a homology between his bigeminal nucleus and the nucleus isthmi. He does not, however, discuss this matter specifically.

CONCLUSIONS

A study of the brains of primitive Mammals in which the tectum is large shows that the nucleus isthmi of Reptiles is also present and well developed in these forms, and is represented by a part of what has usually been called the dorsal nucleus of the lateral fillet. In higher Mammals, the nucleus is much less obtrusive in association with the diminished importance of mesencephalic centres generally. It is probable, also, that the ventral nucleus of the lateral fillet of mammals is the equivalent of the diffuse collection of cells found among the fibres of the lateral fillet in Reptiles and which has there been termed the "nucleus of the lateral fillet." The main part of the medial geniculate body of Mammals is developed as a caudo-ventral extension of the main sensory nucleus of the thalamus, drawn out, it would appear, under the neurobiotactic influence of auditory impulses which pass up to it from caudal levels.

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EXPLANATION OF PLATE I

Fig. 1. Horizontal section of the diencephalon of a 92 mm. human embryo. ×20.
B.i. inferior brachium. *C.m.* centre median nucleus. *C.p.* posterior colliculus. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *V*, ventral nucleus of thalamus.

Fig. 2. Lateral view of mid-brain and diencephalon of *Tarsius*. ×5.
C.a. anterior colliculus. *C.p.* posterior colliculus. *Cr.* crus cerebri. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *N.i.* nucleus isthmi. *T.ac.* tuberculum acousticum.

Fig. 3. Coronal section of mid-brain of *Lacerta viridis*. × 25.
C.p. posterior colliculus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *T.* tectum. *IV*, trochlear nerve.

Fig. 4. Coronal section of mid-brain of *Macroscelides*. ×18.
B.i. inferior brachium. *C.a.* anterior colliculus. *C.p.* posterior colliculus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *IV*, trochlear nerve.

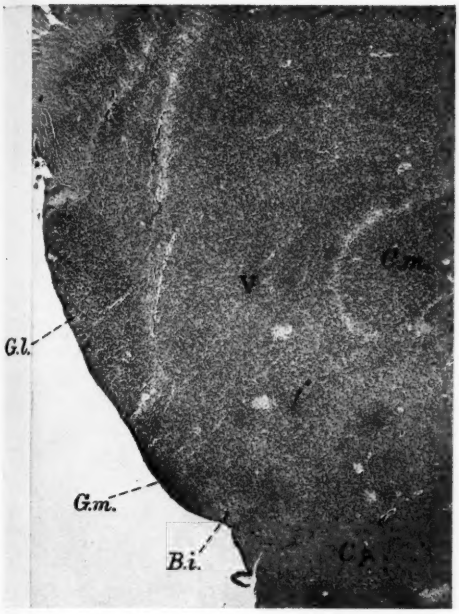


Fig 1.

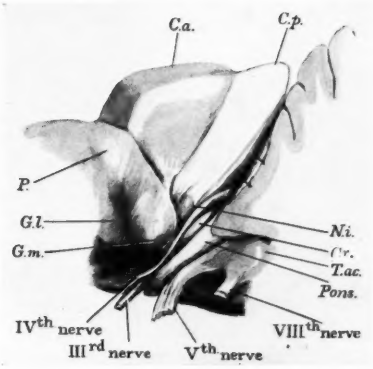
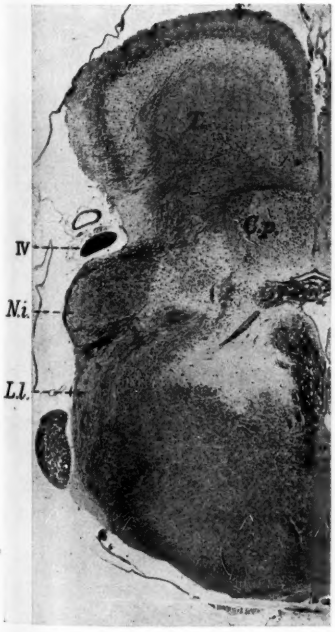


Fig. 2.



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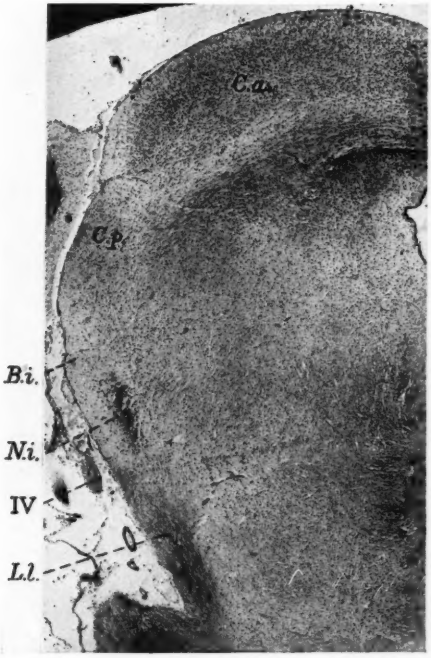

Fig. 4.

THE EXTERNAL CHARACTERS OF AN AUSTRALIAN FOETUS

By FREDERIC WOOD-JONES
Melbourne

The specimen described here was presented to the Anatomical Museum of Melbourne University by the late Sir Baldwin Spencer in 1912. By him it was obtained at Port Darwin; and if it be not now, as its original label described it—"probably the only one in existence"—it is certainly one of no more than two or three that have ever been preserved.

Fig. 1. Female Australian foetus from Port Darwin.

The preservation is not perfect; some degree of maceration of the superficial tissues had evidently taken place before the foetus was hardened with

formalin, but this does not materially interfere with a satisfactory investigation of all the essential external characters. The foetus is a female and both from the general state of development and from body measurements may be taken as being at about the 17th or 18th week of intra-uterine life.

Measurements. In the following tables of measurements and indices I have included for comparison those of a Portuguese foetus slightly larger and those of a Chinese-Hawaiian slightly smaller. The measurements of this comparative material were taken during the routine examination of foetuses of various races at the University of Hawaii.

Table of measurements

Measurement	Australian aboriginal	Portuguese	Chinese-Hawaiian
Suprasternale—symphysion	70	82	67
Symphysion—umbilicus	15	—	—
Vertex—sole	240	260	198
Vertex—coccyx	162	178	136
Total fore-limb	123	112	84
Arm	45	46	36
Forearm	43	35	27
Hand	35	31	21
Total hind-limb	117	108	82
Thigh	55	51	36
Leg	51	46	35
To sole of foot	11	11	11
Width of shoulders	61	73	58

Table of indices

	Australian aboriginal	Portuguese	Chinese-Hawaiian
$\frac{\text{Arm and forearm}}{\text{Trunk length}}$	126	99	94
$\frac{\text{Upper extremity}}{\text{Trunk length}}$	176	136	125
$\frac{\text{Thigh and leg}}{\text{Trunk length}}$	151	118	106
$\frac{\text{Lower extremity}}{\text{Trunk length}}$	167	131	122
$\frac{\text{Arm and forearm}}{\text{Leg and thigh}}$	83	83	88
$\frac{\text{Upper extremity}}{\text{Lower extremity}}$	105	104	102

From an examination of these measurements and indices it is at once apparent that the great relative length of the limbs, which characterises the adult Australian aborigine, is already well established at this early stage. Moreover, it is manifest that though the limbs are of abnormal length, the upper extremity/lower extremity ratio remains normal. It will be noticed that while both fore-limb and hind-limb of the Australian foetus are considerably longer than the corresponding members of the larger Portuguese foetus, the intermembral index is practically the same in the two cases.

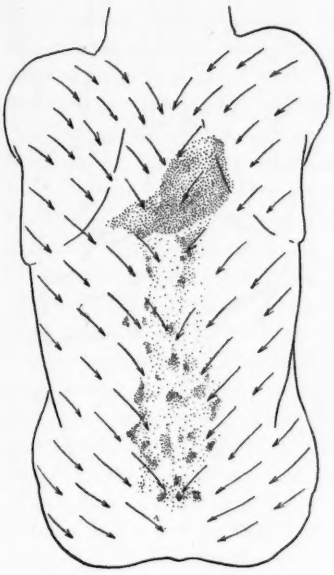

Fig. 2. Distribution of hair tracts and deep pigment on the back.

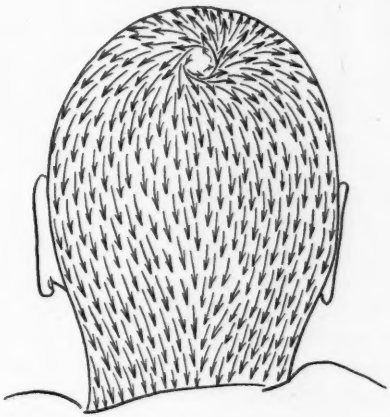

Fig. 3. Hair tracts of the posterior surface of head and neck.

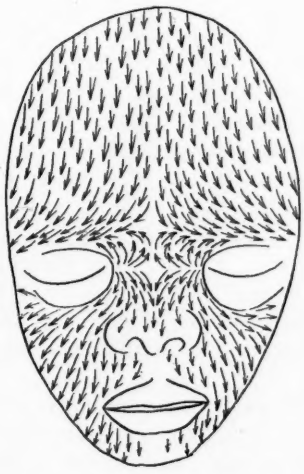

Fig. 4. Hair tracts of the face.

Fig. 5. The form of the left ear and the hair tracts.

Fig. 6. Characters of the face.

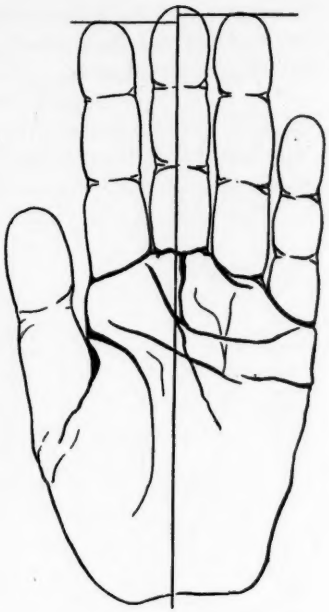

Fig. 7. Left hand, palmar aspect.

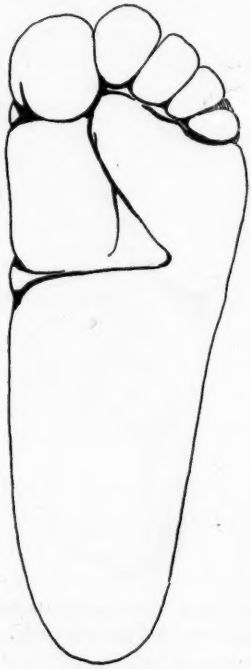

Fig. 8. Sole of left foot.

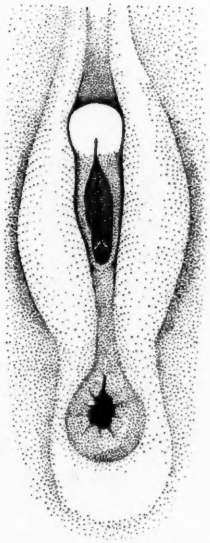

Fig. 9. The external genitalia.

Pigmentation. The foetus has been preserved in formalin and subsequently transferred to spirit and glycerine. After its 20 years' immersion in formalin its coloration differs but little from that of a formalin-preserved white foetus of a similar stage of development. It is rather more yellow than is usual in the case of the European foetus, and though the lips are obviously dusky, the external genitalia remain of the ordinary body colour.

The deep pigment system, which has received the varying names of "mongolian mark," "kinderfleck," "tache pigmentaire," "tache blue," and many others, is well developed. The deep pigment is present as scattered blotches disposed along the vertebral column from the sacral to the interscapular region, one large patch being situated somewhat asymmetrically between the scapulae (see fig. 2). The so-called Mongolian mark was first observed in babies of the "primordial tribes of North Celebes" by Dr J. G. F. Reidal of Batavia. By him its discovery was communicated to Charles Darwin in a letter written 30 June, 1875. Many years later it was recorded in Japanese infants, and it has since been noted in Chinese (Matigon), Annamites, Siamese and Koreans (Chemin), Malays (Kohlbrugge), Filippinos (Colliquon), Javanese (ten Kate and Baumgarten), the Hovas of Madagascar (Fontoynont), and the Esquimaux of Greenland and Alaska (Hansen, Nansen, Saabye). It is present in Samoans, Hawaiians, Tahitians, Marquesans and Maoris. The American Indians also show the mark and it has been recorded in infants from British Columbia, California, Mexico (Herman), Central America (Starr), Ecuador (Rivet), Peru, Brazil and the Argentine as well as in the Patagonians (Lehmann-Nietsche). Among Europeans it has been noted in Bulgars (Wateff) and rarely among Germans (Adachi), Austrians (Epstein, Sperck), and Italians (Menabuoni). In negroes and negro mixtures it has been recorded in America by Bannerman, although it has, apparently, not been observed in negroes in Africa. It is here recorded for the first time in the Australian foetus.

Hair and hair tracts. Hair is well developed upon the scalp and face and the down hairs are visible on all parts of the body. The hair of the scalp is dark brown, but on the face is, in the preserved foetus, of a distinctly reddish colour. The eyebrows and eyelashes are remarkably well developed, individual hairs of the eyebrows being 8 mm. in length, whilst many of the eyelashes reach 5 mm. The hair tracts are recorded in figs. 2, 3, 4 and 5, and they need no description beyond the statement that they are those of a typical and simple human type.

The facial features. The face of the foetus is unmistakably that of an Australian aborigine. The nasal breadth (*I.A.*) and nasal height (*I.A.*) measurements are practically equal. The features are sufficiently well shown in figs. 1 and 6.

The ear exhibits none of those features that have been described as "pithecoid" (Howard Ayers *et alia*). The apex auriculae is not so well marked as is common in white foetuses, and its site is most clearly indicated by the apical hair point (see fig. 5).

The hand shows a digital formula **3.4.2.5.1.** The thumb is well developed, its tip reaching almost to the middle crease line of the index finger. The crease lines of the palm are normal human, as opposed to pithecoid, in type. The free margins of the nails are well marked (see fig. 7).

The foot has a digital formula of **2.1.3.4.5.** Contrasted with the nails of the fingers those of the toes are mere rudiments, being only apparent as small crescentic thickenings with no free edges (see fig. 8).

The external genitalia are of such basal simplicity and illustrate so well the normal disposition to which I have previously called attention (see this *Journal*, vol. XLVII, p. 73; vol. XLIX, p. 393; vol. L, p. 1, etc.) that it has been thought well to figure them (see fig. 9).

The outer genital folds extend from the pubic region to the sides of the anus, enclosing between them an elongated depression which is limited posteriorly by a well-marked ridge behind the anus. The genital tubercle is prominent and cleft, the margins of its cleavage (inner genital folds) forming the lateral boundaries of the urogenital depression. The opening of the vagina is situated very far back and the hymen is unusually deeply situated. The glans is not yet sculptured from the apical portion of the genital tubercle.

THE DEVELOPMENT OF THE VAGINA IN THE RABBIT

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The development of the vagina is a matter on which observers have come to different conclusions, most especially perhaps as regards the structures from which the organ is formed; and it is now generally considered that among the Mammals the developmental processes, so far as the nature of the structures which take part in them is concerned, show a considerable variation. Bloomfield and Fraser (1) reviewed the literature of the subject, and divided the descriptions of the origin of the vagina into three main classes: (*a*) those which describe the vagina to be a structure totally derived from the Müllerian ducts; (*b*) those which consider the vagina to be mainly Müllerian in its origin, but possessing an additional component derived from the Wolffian ducts at its lower end; and (*c*) those which make the vagina a derivative of the urogenital sinus to a greater or lesser extent. Each of these three modes of development has been considered, at one time or another, to be descriptive of the process which occurs in the human subject.

In the Rodentia, as is well known, the vaginal orifice occupies one of two situations. In the one position, as is exemplified in the rabbit, the vagina opens into the urogenital sinus some distance from the exterior; in the other position, as occurs in the rat, the vagina opens into the vulvar cleft on the external surface of the body. The difference between these forms, the one form being as it were complete and the other incomplete, suggested the possibility that these two forms of rodent vagina might have a different developmental history; and that if this difference were known, it would provide a basis, not only on which to compare the rodent vaginae, but also to establish comparisons with the vaginae of other forms.

The development of the vagina in the rabbit was described by Langenbacker (2), according to whom it is derived entirely from the Müllerian ducts. Neither the Wolffian ducts nor the urogenital sinus make any contribution to its formation. The development of the second form of vagina has been studied by Mijsberg (3) who worked on the rat. He concluded that in the rat the upper part of the vagina is derived from the Müllerian ducts; that the part next below this is formed by the fusion of the lower ends of the Wolffian ducts with the Müllerian ducts on each side and the subsequent union of these two masses with each other across the middle line; while the lowest part of the vagina is a portion of the dorsal wall of the urogenital sinus which has

been separated off from the remainder. The chief difference between these two descriptions is that in the rabbit the Müllerian ducts are said to open directly into the urogenital sinus while in the rat they open into the sinus through the Wolffian ducts and do not of themselves acquire a sinus connection; the absence of the Wolffian element in the rabbit is a striking omission.

Carleton (4) has shown that the epithelium of the vagina of the rabbit differs in the upper and lower parts of the organ. The upper two-thirds is lined with a columnar epithelium, of which some of the cells are ciliated and some are not, while the lower one-third has a stratified squamous epithelial lining. It seemed to me that these two regions in the rabbit vagina, especially after I had observed their relations in a developmental series, might have different derivations in spite of the previous work of Langenbacker. Consequently, in an investigation of the development of the female genital tract in the rabbit I paid particular attention to the formative processes of the vagina.

MATERIAL AND METHODS

In this investigation I have studied female rabbit embryos and foetuses from 18 days of gestation (24 mm. C.R. length) until birth. These were available in serial transverse sections, either of the entire embryo or of the abdomen and pelvis. The vagina was also studied in its post-natal development. As a routine Bouin's fluid was employed for fixation. Where decalcification was necessary 2 per cent. nitric acid in 70 per cent. alcohol was used. The sections were stained either with Delafield's haematoxylin followed by 1 per cent. aqueous eosin or with Ehrlich's haematoxylin and Biebrich scarlet.

RESULTS

At the stage of 24 mm. C.R. length the Müllerian ducts have entered the genital cord but have not yet reached the urogenital sinus. No fusion has occurred between the Müllerian ducts. The Wolffian ducts open on each side into the urogenital sinus lateral to a long low ridge which runs down the dorsal wall of the sinus.

The Müllerian ducts reach the urogenital sinus about the 30-mm. stage. Fusion now occurs between the Müllerian ducts in the caudal one-half of the genital cord resulting in the formation of a simple tube lined with a single layer of columnar epithelial cells (text-fig. 1, 35-mm. stage). The upper limit of this tube is the future cervico-vaginal junction. At its lower end this tube or vaginal anlage is in contact with the epithelium of the dorsal wall of the sinus, there being, however, no communication between its lumen and that of the sinus. On each side, too, at its lower end the vaginal anlage is in continuity with the epithelium of the Wolffian duct just above the opening of this duct into the urogenital sinus.

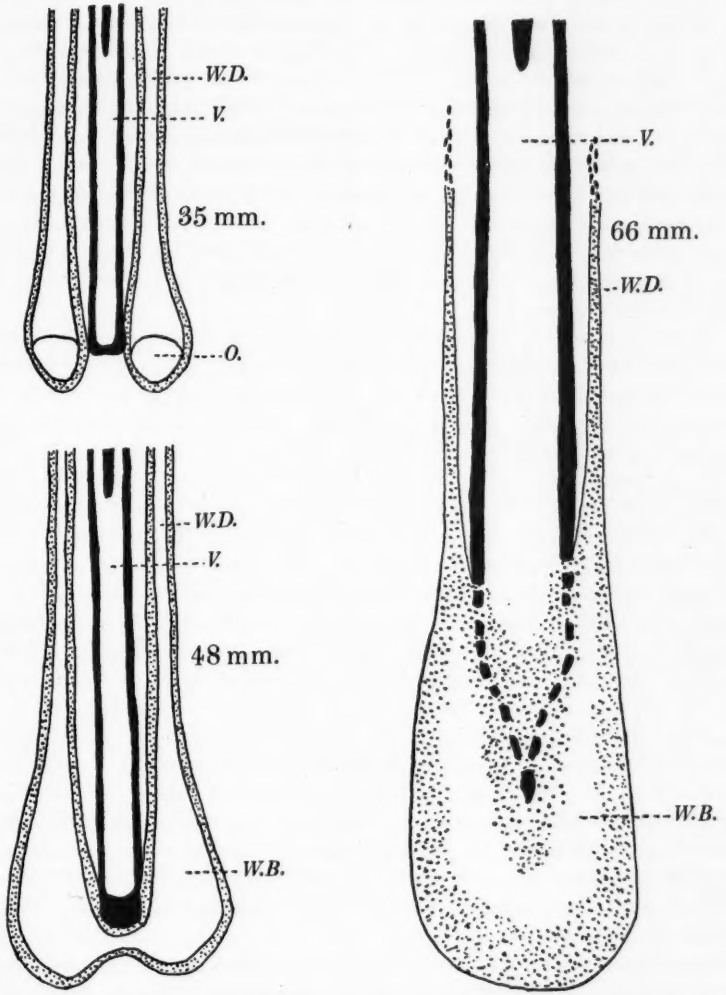

Fig. 1. A diagram showing three stages in the formation of the rabbit vagina based upon graphic reconstructions of the genital cord at the same magnification. *V.* vagina derived from the Müllerian ducts; *W.D.* Wolffian duct; *O.* opening of the Wolffian duct into the urogenital sinus; *W.B.* Wolffian bladder.

The openings of the Wolffian ducts into the urogenital sinus become more and more constricted in later stages, and finally are completely closed off. As this occurs, the lower ends of the ducts become dilated until definite hollow bulbs are formed on them. These retain a solid epithelial continuity with the urogenital sinus below. In their further expansion the Wolffian bulbs extend medially and intervene between the lower end of the vaginal anlage and its connection with the sinus. They eventually communicate with each other across the middle line and in this manner form a barrier between the vaginal anlage and the sinus (text-fig. 1, 48-mm. stage). While these changes are occurring, the extreme lower end of the vaginal anlage has become solid; and it is in continuity with the Wolffian bulbs on each side. On careful examination of this part I am convinced that both Wolffian and Müllerian cells are present in the common knot.

After this time the Wolffian ducts degenerate except in that region where they are related to the vagina (text-fig. 1, 66-mm. stage). This persisting portion of each duct is found to play an extremely interesting part in the formation of the lower end of the vagina. Its rôle is well illustrated in text-fig. 1, 66-mm. stage, and in Plate I, figs. 1–4. At this time the Wolffian ducts are first recognised, as the sections are followed in a caudal direction, in the loose layer of tissue internal to the future circular muscle layer of the vagina. They are quite separate at this point from the epithelium of the vaginal anlage, or from what, as I shall show would be better termed the Müllerian vagina (Plate I, fig. 1). About three-quarters of the way down the vagina the Wolffian ducts pass obliquely caudo-medially and fuse with the epithelium of the lateral wall of the vagina (Plate I, fig. 2). Then the Wolffian ducts are found to break through the lateral wall of the vagina and to proliferate cells into its lumen. These cells are polygonal in form with pale cytoplasm and quite lightly staining nuclei. They thus present a marked contrast to the deeply staining columnar Müllerian epithelium which is seen lying external to them (Plate I, fig. 3). When the Müllerian cells are traced downwards they are found completely to disappear. At this region the Wolffian cells are arranged in the form of two hollow bulbs first placed side by side (Plate I, fig. 4), and then communicating with each other below (text-fig. 1, 66-mm. stage). The epithelial walls of these bulbs are fused below with the epithelium of the urogenital sinus.

After this time, the Wolffian bulbs quickly become solid (75-mm. stage) by proliferation of the cells which form their walls (Plate I, fig. 5). The Wolffian ducts, proximal to the bulbs, are no longer to be recognised as such, except for a small strand of cells which fuses with the vaginal wall at the junction of the solid and hollow portions of the vagina. At birth the lower one-quarter of the vagina is represented by a solid epithelial cord derived from the Wolffian ducts. This epithelial cord is horseshoe-shaped in transverse section and somewhat compressed antero-posteriorly; in this way there is indicated its bilateral origin. Canalisation of this epithelial cord commences

very shortly after birth (Plate I, fig. 6) and this process is completed at the age of five weeks, by which time the animal is 23 cm. in length from vertex to rump. The epithelial cord gives rise by its canalisation to that part of the adult rabbit vagina which is lined with stratified squamous epithelium. This portion is, therefore, Wolffian in origin. The remainder (the upper three-quarters of the adult vagina) is derived from the Müllerian ducts and retains its primitive columnar epithelium.

In the new-born rabbit it was observed that the vaginal mucous membrane projects inwards from the lateral wall of the vagina in the form of a crescentic

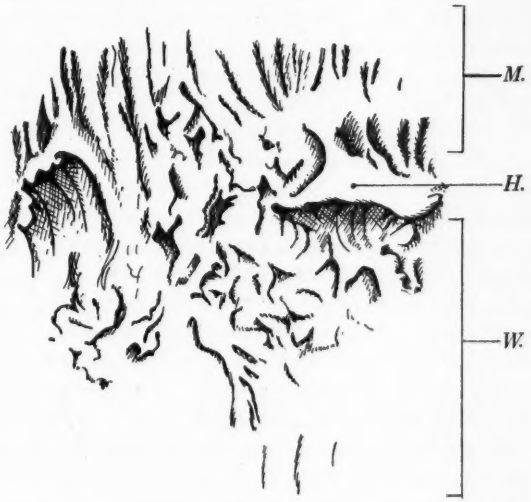

Fig. 2. Drawing of the "hymeneal" folds in the vagina of an adult virgin rabbit, ×8. *H.* hymeneal fold; *M.* Müllerian vagina; *W.* Wolffian vagina.

shelf on each side. This shelf lies just at the junction of the hollow and solid portions of the vagina and, therefore, just above the point where formerly the Wolffian ducts were connected with the vaginal epithelial wall. When the adult virgin rabbit vagina was examined to determine the presence or absence of these folds the condition shown in text-fig. 2 was found. The upper three-quarters of the vagina is beset with vertical ridges arranged parallel to each other. The lower one-quarter shows a number of small folds arranged irregularly and interlacing everywhere with each other. At the junction of these two parts there is, on each lateral wall, a very distinct crescentic fold projecting transversely into the lumen[1]. These folds have been described by

[1] Microscopic examination of these folds shows, that while the muscle and the submucosa of the vaginal wall present distinct differences above and below the fold, the epithelium cannot be said to show a definite alteration in character. This is possibly due to the stage in the oestrous cycle at which this animal was examined.

Owen (5) and although he made no statement regarding their nature, it seems to me possible to regard them as homologous with the hymen of higher forms.

DISCUSSION

The developmental processes which I have found to occur in the formation of the vagina of the rabbit place it in the second class of Bloomfield and Fraser. My preparations do not support the view of Langenbacker that the rabbit vagina is derived only from the Müllerian ducts. On the contrary, the Wolffian contribution is not inconsiderable, amounting to the lower one-fourth of the adult organ. The formation of Wolffian bladders in the rabbit is a very definite phenomenon, and the manner in which they grow medialwards, fuse with each other below the Müllerian vagina and so form a barrier of Wolffian tissue between the Müllerian vagina and the sinus, as well as the actual invasion of the lower part of the Müllerian vagina by Wolffian cells, points clearly to the extensive growth processes which occur at the lower ends of the Wolffian ducts. It should be noted that this growth of the Wolffian bladders does not produce an invagination of the dorsal wall of the urogenital sinus. Increase in length of the lower part of the rabbit vagina seems to be due only to interstitial growth of the Wolffian bladders.

There has been no indication in my preparations that the urogenital sinus makes any contribution to the lower end of the vagina in the rabbit in the manner in which it forms the lowest part of that organ in the rat. It would appear, then, that there are two main modes of formation of the vagina in the Rodentia. In all rodents the upper part of the vagina is Müllerian in origin; the next portion is formed from the Wolffian ducts. Then in those rodents in which the vaginal orifice is on the outer surface of the body, the urogenital sinus contributes to the formation of the lowest part of all.

In the mode of origin of the vagina there would seem to be certain similarities in the formation of the single vagina of the rodents and the lateral vaginae of the marsupials. According to Buchanan and Fraser (6) each lateral vagina of marsupials is Müllerian in the upper two-thirds; the lower one-third is in some forms Wolffian alone, in others it is formed from the united Wolffian and Müllerian ducts, and yet in others it is derived from an outgrowth of the urogenital sinus. Now these facts would seem to indicate that in the rodent vagina there are retained the same sources of origin as the lateral vagina of the marsupials. They would also support the view that the single rodent vagina represents the fusion (in its lower part at least) of the paired lateral vaginae of the Marsupialia.

The "hymeneal" folds which I have figured in the vagina of the rabbit have a situation which requires further comment. They are found just above the point where the Wolffian ducts formerly fused with the lateral epithelial wall of the vagina and so they bear the same relation to the Wolffian ducts as does the hymen in the human subject (cp. Bloomfield and Fraser (1)). If it

be held that in the human subject the vagina is derived only from the Müllerian ducts, it is then evident that there is a structure contributing to the formation of the rabbit vagina which is not represented in that organ in the human subject. Further, that this loss of the Wolffian component in the human vagina is due to the peculiar invagination of the dorsal wall of the urogenital sinus by the lower end of the vagina that occurs in the human female. The Wolffian ducts are in this manner excluded from the vagina, and, if they persisted, would open on the distal surface of the hymen.

SUMMARY

1. The development of the vagina has been investigated in the rabbit (*Lepus cuniculus*).

2. The Müllerian ducts reach the urogenital sinus at the 30-mm. stage and quickly fuse together in the lower one-half of the genital cord. This results in the formation of a simple epithelial tube which is the anlage of the upper part of the vagina.

3. The Wolffian ducts lose their openings into the urogenital sinus (about the 40-mm. stage) and become dilated at their lower ends in the form of two little bladders; and these grow medially between the lower end of the Müllerian vaginal anlage and the urogenital sinus until they meet in the middle line and fuse with each other. A communication is, in this manner, formed between the bladders across the middle line.

4. The Wolffian ducts degenerate except in that portion which is related to the vagina. At the 66-mm. stage the Wolffian ducts are found to fuse with the lateral wall of the Müllerian vagina at the junction of the upper three-quarters with the lower one-quarter of the genital cord. Then the ducts break through the wall of the Müllerian vagina and proliferate cells into its lumen. Lower down, the Wolffian bulbs grow and become solid by proliferation of the cells forming their walls.

5. There is formed, in this manner, a solid epithelial cord which is canalised after birth and so gives rise to the lower one-quarter of the adult vagina. This portion of the vagina is Wolffian in origin and in the adult is that part lined with stratified squamous epithelium. The upper Müllerian part of the vagina retains its primitive columnar lining.

6. Just above the opening of the Wolffian duct into the vagina there is formed on each side a crescentic fold projecting into the lumen. This fold persists when the Wolffian duct has completely vanished. If this fold is regarded as homologous with the hymen it is then suggested that the rodent vagina possesses a component that is no longer present in the human subject; further, that this Wolffian component of the rodent vagina has been exteriorised in the human owing to the invagination of the dorsal wall of the urogenital sinus by the lower end of the developing vagina.

7. The close similarity between the components of the single vagina of the rodents and the lateral vaginae of the marsupials is indicated.

I should like to thank Prof. Walmsley for his interest and criticisms during this investigation. He suggested the problem to me in the first place and he has aided me greatly during its course by his kind advice. I am indebted to Dr R. H. Hunter for the drawing of text-fig. 2.

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EXPLANATION OF PLATE I

Fig. 1. Transverse section at the junction of the middle and caudal thirds of the genital cord of a 66 mm. female rabbit embryo, × 120. 1, Müllerian vagina; 2, Wolffian duct.

Fig. 2. Transverse section of the same embryo 90 microns caudal to the preceding, × 120. The Wolffian ducts are shown fusing with the lateral walls of the Müllerian vagina. 1, Müllerian vagina; 2, Wolffian duct.

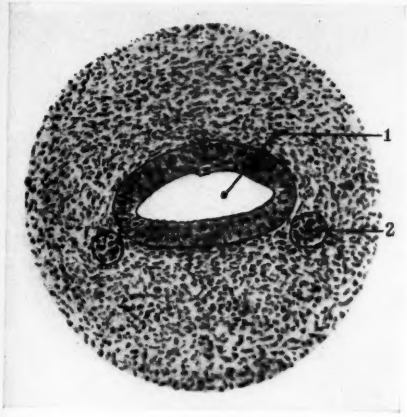
Fig. 3. Transverse section of the same embryo 45 microns further caudal, × 120. Cells derived from the Wolffian ducts are seen proliferating into the lumen of the Müllerian vagina. 1, Müllerian vagina; 2, Wolffian duct; 3, Wolffian cells filling up the lumen of the Müllerian vagina.

Fig. 4. A section 45 microns caudal to that shown in fig. 3, and at the same magnification. The Müllerian vagina as such has disappeared and in its place are seen the two Wolffian bulbs. A few Müllerian cells are to be seen on the dorsal wall of the vagina. 1, Wolffian bulb; 2, Müllerian epithelium.

Fig. 5. Transverse section through the lower part of the genital cord of a 75 mm. female rabbit embryo, × 120. Proliferation of the Wolffian cells has given rise to a solid epithelial vaginal cord.

Fig. 6. Sagittal section through the pelvis of an 11 cm. rabbit, × 27·5. This shows the two component parts of the vagina. The canalisation of the lower solid cord has just commenced. 1, Müllerian vagina; 2, epithelial cord derived from the Wolffian ducts now showing the commencement of canalisation; 3, urethra.

The uniformity of the colour of the sections after staining required the insertion of a boundary line around the epithelium; this is not intended to represent the basement membrane.



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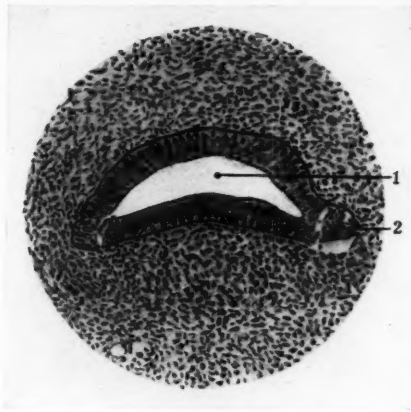

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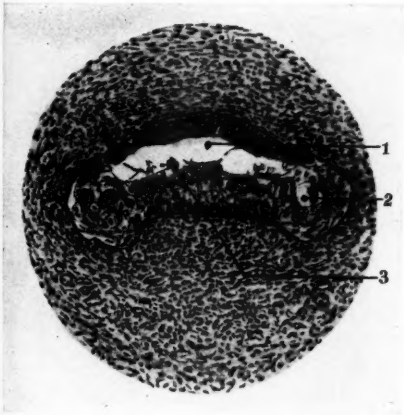

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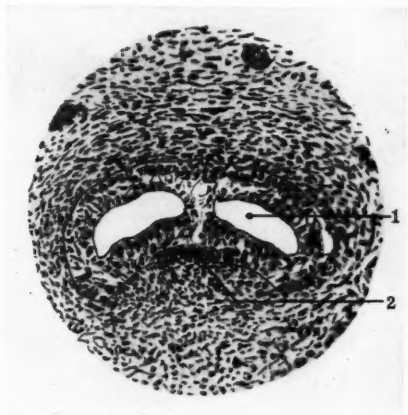

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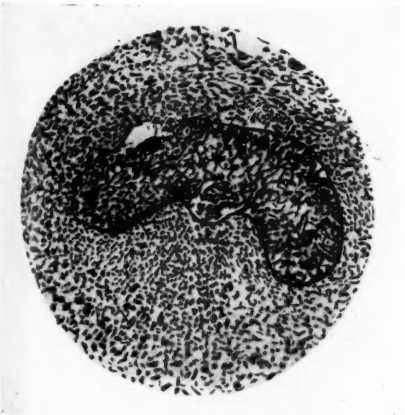

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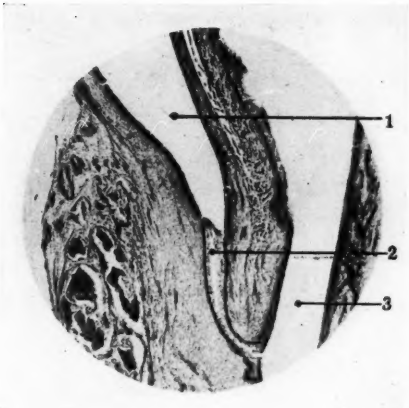

Fig. 6.

CHORIO-ALLANTOIC GRAFTS OF SINGLE SOMITES AND OF THE UNSEGMENTED PARAXIAL REGION OF THE TWO-DAY CHICK EMBRYO[1]

By P. D. F. MURRAY (*Smithson Research Fellow*)
and D. S. SELBY

INTRODUCTION

In 1925, Hoadley (*J. Exp. Zool.* vol. XLII) described chorio-allantoic grafts of parts of the somitic regions of chick embryos. In some of the grafts the spinal cord was present, in others strings of somites were taken from one side of the embryo and grafted without any nervous tissue. In both types of graft the somitic tissue differentiated, forming cartilage and muscle, and it appeared that the presence or absence of nervous tissue was without effect on the differentiation. The object of the present experiments was to test the ability of single segments of the paraxial region of the embryo and of the unsegmented paraxial region to differentiate after grafting in the chorio-allantois. Grafts of larger masses of segments and grafts of entire metameres were also made.

The following terms are used in this paper and perhaps require explanation. *Paraxial region:* that region of the embryo which contains the somites, the unsegmented mesoderm from which somites are derived by segmentation, and the ectoderm and endoderm above and below these. *Paraxial mesoderm:* the mesodermal constituents of the paraxial region. *Segment:* a fragment or region of an embryo consisting of a single somite with the associated overlying ectoderm and underlying endoderm. *Unsegmented paraxial region:* a fragment or region of an embryo consisting of the unsegmented paraxial mesoderm lying posterior to the somites with associated overlying ectoderm and underlying endoderm. *Metamere:* a fragment or region of an embryo consisting of a pair of somites of opposite sides with the axial organs between them and with the associated overlying ectoderm and underlying endoderm.

METHOD

The method was that usual in chorio-allantoic grafting and needs no description. The single segments required for grafting were obtained as follows. The donor chicks, which had in all cases been incubated for about 2 days, were placed upon a flat sheet of glass in saline. The segments of one side were isolated by two longitudinal cuts, one medial to the somitic series separating it from the axial organs and the other lateral, separating it from the lateral

[1] This work was done in the Department of Zoology of the University of Sydney in 1928.

plate. The nephrotome usually lay lateral to this incision but was sometimes on its medial side, in which case some nephrotome material was generally included in the graft. The string of segments, freed posteriorly by a transverse cut, resembled a tapeworm and individual segments were cut off posteriorly as required, much as one might amputate the segments of the worm. Grafting was carried out on the point of a needle. For the other kinds of graft modifications of the same method were used.

The grafts were allowed to remain undisturbed in the host for a period of from 7 to 10 days. When the eggs were opened for recovery of the graft any thickening of the chorio-allantois, however small, was fixed, and nearly all the material fixed was sectioned. The only specimens not sectioned were those in which examination after clearing showed definitely that no graft was present. It was thus possible to be certain that at the most not more than a very small number of the little grafts escaped discovery. Fixation was in Carnoy's fluid, staining with Delafield's haematoxylin and eosin.

Two important points should be mentioned here:

(1) All the grafts contained material derived from all three germ layers. Thus, the grafts referred to as "single segments" each contained, in addition to the somite itself, a tiny piece of overlying ectoderm and of underlying endoderm.

(2) In all cases the age of the donor chick was approximately 48 hours. The precise age in hours was not recorded because of the greater precision attained by counting the number of somites.

DESCRIPTIVE SECTION

Grafts of several different kinds were made. The following table states the nature of the grafts, the number of host eggs which survived the operation and the number of successful grafts obtained.

Nature of graft	No. of hosts surviving	Successful grafts
(1) Single segments	111	6 perhaps 7 (5·4 %, perhaps 6·3 %)
(2) Segments in strings of three or more	41	8 (19·5 %)
(3) The unsegmented paraxial region entire or in pieces equal to or greater than one-half	20	6 (30 %)
(4) Pieces of unsegmented paraxial region smaller than one-half	7	0
(5) One or more segments of one side with all or half the associated axial organs	10	3
(6) One segment of both sides with the associated axial organs (complete metameres)	32	19 (59·4 %)

In the following sections the numerical data given at the head of each description of a graft are to be interpreted thus: The number of the individual graft is given in italics. This is followed by figures indicating which segment in the series was grafted and the total number of somites in the embryo.

Thus, the figures S18/27–8SS mean: the graft was one of the 18th pair of segments of an embryo having 27 or 28 pairs of somites. Entire unsegmented paraxial region /18SS means that the graft was the entire unsegmented paraxial region of an embryo having 18 pairs of somites.

Isolated segments (fig. 1 *a*)

21, No. 16. S18/27–8SS. Nine days as a graft.

The graft consisted of three components of which only one had attained to sufficiently advanced differentiation to render definite histological identification possible. This was a rounded nodule of well-developed cartilage enclosed

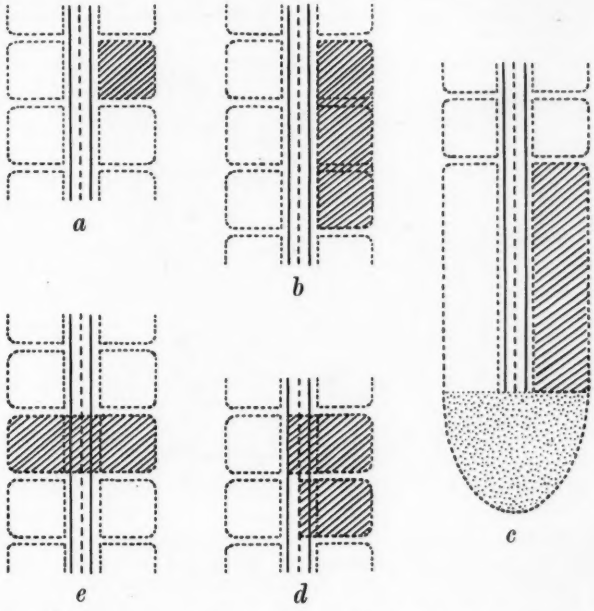

Fig. 1. Diagram illustrating the nature of the grafts. *a*, *b*, *d* and *e* represent parts of the somitic region, *c* represents the posterior end of an embryo. The regions used as grafts are indicated by diagonal shading.

in a fibrous perichondrium. There was no ossification and no cartilage resorption.

27, No. 7. S9/22SS. Nine days as a graft.

The graft consisted of a piece, roughly rectangular in form, of very well-developed cartilage. It was enclosed in a feeble perichondrium. There seemed to have been no ossification and cartilage resorption had not set in. No other tissue appeared to have differentiated from the graft, but owing to the destruc-

tion of several sections in the series, it was impossible to be quite certain of this.

35, No. 6. S20/38SS. Eleven days as a graft. Donor incubated 65 hours.

This graft was another nodule of cartilage enclosed in a thick fibrous perichondrium. Close to the cartilage was a small bundle of material which was almost certainly voluntary muscle.

36, No. 7 (fig. 2). S14/30SS with a tiny bit of S15. Nine days as a graft.

This again was a piece of hypertrophied cartilage. It was evident that a large part of the original cartilage had suffered resorption. The entire structure, both the existing cartilage and the region of resorption, was enclosed in a sheath of perichondral bone. There was no endochondral ossification.

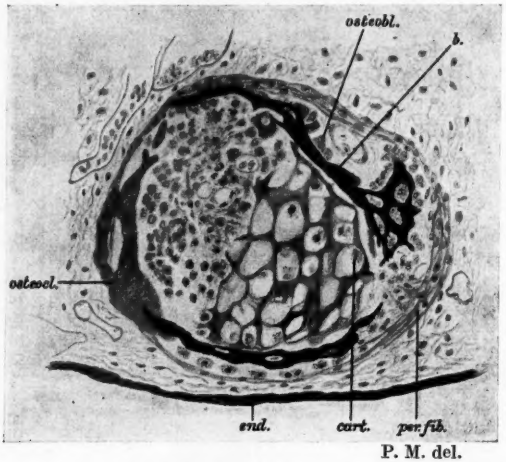

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Fig. 2. Graft 36, No. 7. A nodule of cartilage undergoing resorption and partly invested in periosteal bone. *b.* bone; *cart.* cartilage; *end.* endodermal epithelium of chorio-allantois; *osteobl.* osteoblast; *osteocl.* osteoclast; *per fib.* fibrous layer of periosteum.

36, No. 9. S12/30SS with a fragment of either S11 or S13. Nine days as a graft.

This is another nodule of cartilage. Perichondral ossification had just begun but there had been no resorption of cartilage. Associated with the cartilage were a number of groups of voluntary muscle fibres.

In addition to the above grafts there was one other case in which a tissue resembling cartilage was present, but the correct interpretation of which is uncertain.

Unilateral series of segments (fig. 1 *b*)

Forty-seven hosts survived the operation and from these nine grafts were obtained. Four of the nine contained each a nodule of cartilage, and two of

these, with two others, contained also voluntary muscle. Bone occurred in two grafts, in one of which it was present as a separate nodule and cartilage was absent, while in the other there was both a separate nodule of bone and also perichondral bone around a nodule of cartilage.

Two grafts contained epithelial tubes evidently representing sections of the alimentary tract; in one case the epithelial tube had a thin coating of smooth muscle.

Tubules which were probably derived from accidentally included fragments of nephrotome were found in two grafts. One graft consisted of a feather and nothing else.

In no case was there any indication of segmentation or any suggestion of normal anatomy.

Grafts of the unsegmented paraxial region (fig. 1 *c*)

These grafts consisted of the unsegmented paraxial mesoderm with its overlying ectoderm and underlying endoderm.

6, No. 10. Entire unsegmented paraxial region of one side /18SS. Nine days as a graft.

The mesodermal component of the graft had differentiated into cartilage, muscle and kidney. There was one large piece of cartilage of rather irregular form and one small nodule. The structure of the larger piece suggested its formation by the coalescence of several smaller components. There was no sign of osteogenesis. Only a small amount of voluntary muscle was present. It was evident that a portion of the nephrotome was included in the graft for there were two masses of nephric tissue. The endoderm formed a section of gut.

9, No. 13. Entire unsegmented paraxial region of one side /20SS. Ten days as a graft.

This was a well-differentiated graft showing a section of alimentary tract, cartilage and voluntary muscle. The cartilage was in two pieces widely separated from one another; one piece was considerably larger than the other. There was no bone. The voluntary muscle which was attached to the larger piece of cartilage showed little regularity in the arrangement of its fibres.

22, No. 2. Entire unsegmented paraxial region of one side /20SS. Eight days as a graft.

In this graft the derivatives of the paraxial mesoderm were represented by a rather large nodule of cartilage of somewhat irregular form and with little or no ossification.

In the neighbourhood of the graft there was a big area of inflammation and degeneration; it is possible that part of the graft was included in this region and destroyed.

28, No. 6. Entire unsegmented paraxial region of one side /14SS. Eight days as a graft.

The only derivative of the axial mesoderm which was present in this graft was a small nodule of cartilage with perhaps a very little ossification. In addition there were tubes which probably represent alimentary tract and kidney.

29, No. 1. Entire unsegmented paraxial region of one side /21SS. Ten days as a graft.

Scattered through this graft were five nodules of cartilage. Of these two were joined by a constriction probably representing a secondary fusion. In addition to the cartilage there were present voluntary muscle, a large vesicle lined with skin and having large feathers, and nephric tubules. There was a considerable quantity of voluntary muscle, some of the fibres associated with one of the nodules of cartilage, others having no relation to the cartilage at all. The alimentary tract, if it was present at all, was represented by a few small tubes that cannot be positively identified.

There was no trace of anatomical normality in the arrangement of the cartilages and muscle fibres.

25, No. 1. Entire unsegmented paraxial region of one side probably plus S25/25SS. Eight days as a graft.

The graft consisted of cartilage, voluntary muscle, nephric material and skin. There was one very large piece of cartilage of rather irregular form, suggesting its formation by the coalescence of several nodules. The skin was in the form of two connected vesicles which contained feathers. There were several masses of nephric material.

Segmental material of one side with axial organs (fig. 1 *d*)

Nine hosts survived the operation and three grafts were obtained. Two of these consisted of a single segment of one side with half the axial organs opposite to it, while the third consisted of two segments of one side with the entire axial organs opposite to them. All the grafts contained cartilage and central nervous tissue, two contained perichondral bone and one (that in which the graft contained two somites) a large quantity of voluntary muscle. In no case was there any suggestion of normal gross anatomy. The nervous component of the grafts developed as quite irregular masses of nervous material giving off bundles of nerve fibres. Save for a tendency for the cell-bodies to be placed centrally in the masses with the fibres peripheral to them, and for the occurrence in one case of an eccentrically situated neurocoele, the elements of the spinal cord showed no such regularity of arrangement as is characteristic of the normal organ. The neurocoele was found in the graft which contained two somites and the entire axial organs opposite to them;

it was hardly to be expected that a neurocoele would appear in the other two grafts.

Entire metameres (fig. 1 *e*)

There is no need to describe these grafts in detail. Their interest lies chiefly in the fact that 59·4 per cent. of the surviving hosts contained grafts, a figure to be compared with 5·4 per cent. for the single segments, and 19·54 per cent. for strings of segments.

Most of the nineteen grafts contained cartilage, muscle, and central nervous tissue, all in a highly differentiated condition. In a few cases the muscle failed to differentiate and one graft consisted merely of a mass of degenerate material in which could be seen pieces of cartilage. Only one graft contained notochord.

The nervous tissue was usually tubular, but the neurocoele might be partly or entirely suppressed. Spinal ganglia were often recognisable. The cartilage in a few cases resembled a vertebra, to the extent of making a more or less complete ring round the nervous material, and in some it was perforated by foramina through which issued spinal nerves. Occasionally there were projections from the main mass of cartilage strongly suggestive of transverse processes.

In addition to these tissues it was not uncommon to find in the grafts sections of tubular gut, skin and masses of nephric tubules. The presence of the latter of course, was due to the occasional accidental inclusion in the graft of a part of the nephrotome.

DISCUSSION

The results are here discussed under two headings: histological differentiation and anatomical differentiation.

Histological differentiation

Grafts of single segments and grafts of the entire unsegmented paraxial region and of fragments greater than half of this showed advanced histological differentiation of cartilage, bone and muscle. Hence the single segment and the unsegmented paraxial region are shown to be able to self-differentiate to the extent of producing these tissues in the absence of the remainder of the embryo. Grafts of smaller pieces of the unsegmented paraxial region failed to differentiate but since there were only twelve attempts with seven survivals no conclusion can be drawn.

The self-differentiation of the isolated segments and of the unsegmented paraxial region suggests that these structures contain cells which are determined for, or at least biassed towards the formation of the group of tissues: cartilage, muscle and bone. While it does not prove the existence of some cells specifically and individually determined for cartilage formation, others for bone, and still others for muscle formation, the production of both cartilage and

muscle by the same graft renders it probable that both somites and unsegmented paraxial mesoderm were at grafting already mosaics with different regions predetermined for the formation of different tissues. It is, however, possible that the grafts were equipotential systems the fates of whose particular parts were determined by extrinsic conditions. While this remains uncertain, it is evidently impossible to say anything of the determination of single cells at grafting; for if the somite and unsegmented paraxial mesoderm are equipotential systems, the cells must be equipotential with one another, while if these structures are mosaics, the determining factor might lie either within the individual cells so that these would each be determined for a particular differentiation or in some kind of supracellular morphogenic field, so that individual cells, if transferred from one part of the mosaic to another, might show themselves to be indifferent and equipotential.

Grafts of single segments were successful in 5 or 6 per cent. of cases in which the host survived the operation, while grafts of strings of three or more segments were successful in 19·5 per cent. of cases. The explanation of this difference lies evidently in the size of the two kinds of graft. The part of the graft which suffers injury at operation is the surface and, since the ratio of surface to volume increases as the size of the graft decreases, it follows that the smaller the graft the greater the proportion of its material which suffers injury. But a string of three segments is of roughly the same size as a single metamere, yet of the latter 59·4 per cent. of surviving hosts contained grafts, compared with 19·5 per cent. of the former; this difference must be due to some factor other than size. The nature of this factor is unknown; it may be the presence of the nervous system or it may be that a metamere is in some way a more completely autonomous unit than is a string of segments. The former view is rendered less probable by Hoadley's finding that innervation had no recognisable effect on the differentiation of larger masses of somitic material.

It should here be repeated that all the grafts contained not only the intended mesodermal component but ectoderm overlying it and endoderm underlying it. A possibility that the differentiation of the mesoderm may be dependent on the presence of this ectoderm or endoderm is thus not entirely excluded. There is, however, no evidence for this and it is rendered improbable by the fact that the frequent failure of ectoderm and endoderm to develop in no way impeded the differentiation of the mesoderm.

Anatomical differentiation

(1) Grafts of single segments and of strings of segments formed amorphous nodules of cartilage; in no respect was there any approach to normal gross anatomy and grafts of strings of segments showed no indication of segmentation. Since the somites were already, of course, segmentally separated from

one another this was probably due to unfavourable conditions in the chorio-allantois and to the tendency of cartilages to fuse with one another. Hoadley found that in his grafts of strings of somites, cartilages developed which sometimes resembled parts of vertebrae.

(2) Grafts of the unsegmented paraxial region, whether entire or in large fragments, similarly showed no approach to normality of anatomical form. There were, however, suggestions of segmentation. One graft formed five separate pieces of cartilage, two formed two pieces, while the remaining four each formed one piece. In two of the latter four, however, and in the larger cartilage of one graft that had two pieces, the appearance suggested that the existing cartilages were formed by the coalescence of several smaller pieces. It thus seems probable that the grafted unsegmented paraxial mesoderm tended to produce several pieces of cartilage, perhaps indicating an attempt at segmentation. This would mean that mesodermal segmentation was brought into existence by factors already latent in the unsegmented paraxial mesoderm rather than by action upon it of factors extrinsic to it. It is, however, possible, though perhaps improbable, that the production of several cartilages may have been due to the disruption of single anlagen by mechanical factors in the chorio-allantoic environment.

(3) Grafts of entire metameres showed a better approach to the normal anatomical arrangement of tissues than any of the other types of graft. This is to be expected, since, at transplantation, the broad anatomical arrangement was already laid down and was not disrupted by the operation, as it was in all the other types of graft. Differentiating somites may reasonably be expected to form some kind of vertebra-like structure if they lie on each side of a section of a spinal cord.

SUMMARY

1. Chorio-allantoic grafts were made of single segments, unsegmented paraxial regions, strings of segments and entire metameres less the regions lateral to the somites, of 2-day chick embryos.

2. Differentiation occurred in all these types of graft. Single segments, strings of segments, and unsegmented paraxial regions produced cartilage, bone and muscle. Entire metameres produced in addition, nervous tissue.

3. The presence in the grafts of overlying ectoderm and underlying endoderm led to the occasional development of skin and of sections of alimentary tract. Accidental inclusion of the nephrotome in the grafts led in many cases to the development of nephric tubules.

4. There was no development of anything even remotely approaching normal anatomy in any kind of graft except those of complete metameres in which structures resembling very abnormal vertebrae were sometimes formed.

5. It is concluded that:

(*a*) The isolated unsegmented paraxial region and isolated segment are

able to self-differentiate to the extent of producing cartilage, bone, and muscle. This suggests strongly that both somites and unsegmented paraxial mesoderm were at the time of transplantation, already predetermined mosaics.

(*b*) An entire metamere has a greater viability as a graft than a string of segments of equal size. The reason for this is not known.

(*c*) It is probable that the segmentation of the paraxial mesoderm is due to the activity of intrinsic factors which are already present before the onset of segmentation.

THE CAUSE OF TORSION OF THE HUMERUS AND OF THE NOTCH ON THE ANTERIOR EDGE OF THE GLENOID CAVITY OF THE SCAPULA

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It is a well-known fact that in the higher Primates, as compared with other groups of animals, the humerus has undergone a twist so that the superior articular surface, which in most Mammals looks backwards, has come in them to look backwards and medially or almost entirely medially. To this feature the name "torsion of the humerus" has been applied. The amount of this torsion is measured by taking the long axes of the articular surfaces at the upper and lower ends of the bone and noting the angle formed by these two lines when the bone is looked at from above. In most Mammals these lines meet at about a right angle, but in the higher Primates the upper axis has rotated, its posterior end moving medially and its anterior end laterally, so that the angle between it and the lower axis is more than a right angle.

The amount of this torsion occurring in many different groups of Mammals and Man has been measured, and it is found to increase steadily as we pass upwards through the Primates from the lower to the higher members of the group. Even within the various groups or races of Man it is found to vary considerably, being less in primitive races and greater in the more civilised ones. The following table, compiled mainly from Martin's *Lehrbuch der Anthropologie*, gives the average values of this angle in different groups of Man and Mammals and illustrates the gradual increase of the torsion as we ascend the Primate series.

Carnivora	94·9°	Gorilla	141·1°
Mandrill	98·3°	Australian natives	134·5°
Barbary Ape	106·3°	Melanesian	139·0°
Semnopithecus	110·0°	Negro	144·2°
Hylobates	112·0°	Modern Swedes	163·9°
Orang-utan	120·2°	Modern Swiss	164·0°
Chimpanzee	128·0°	Modern French	164·0°

It will be noticed that there is some overlap between the higher Primates and primitive races of Man, but, otherwise, the amount of torsion of the humerus increases as we pass up the series.

Some other interesting facts about the amount of torsion found in different humeri are mentioned by Martin in the work already quoted. Thus the torsion

is greater in female than in male skeletons; it is greater in weak than in strong skeletons; and, in the same individual, it is generally greater in the bone from the left side than in that from the right.

Yet, in spite of the fact that the angle of humeral torsion has been accurately measured in very many animals by many different observers, there appears to be some uncertainty about the nature of the torsion itself. Duckworth, in a footnote, states: "It may be remarked that no consensus of opinion appears to exist as to the exact nature of this torsion nor as to which parts are affected and which are unaffected by the process, i.e. whether the shaft is unaffected and the torsion is produced only at the articular ends, or whether all parts are involved. No spiral fibres are seen in the structure of the bone, and as for the spiral course of the musculo-spiral nerve, it is such that it represents torsion in exactly the opposite direction to that which is described as having occurred. Besides the other nerves show no sign of a spiral course (1)."

In addition to what Duckworth states above, it may be said that as yet no satisfactory explanation has been offered as to how this twisting of the humerus in the higher Primates has been brought about. It is, of course, known that the change in the position of the superior articular surface of the humerus corresponds with changes in the pectoral girdle, and especially with changes in the position of the scapula. For in the higher Primates the transverse diameter of the thorax becomes relatively greater and the antero-posterior diameter relatively less. This fact is correlated with the gradual assumption of the upright attitude, and produces a change in the position of the scapula which is pushed back, as it were, by the lateral expansion of the chest. In Man, therefore, the scapula lies more nearly at right angles to the median plane of the body than in the lower Primates, and the glenoid cavity is directed more laterally. Accompanying this change in the way the glenoid cavity faces, we find a corresponding change at the superior articular surface of the humerus which is turned gradually round till it looks more medially than backwards. But these facts leave unexplained the exact mechanism by which the head of the humerus was made to rotate. It seems, therefore, that not only are we ignorant of the mechanism by which torsion of the humerus was produced, but also we are very uncertain as to the exact nature and site of the torsion itself.

These last two points must be cleared up before we can be in a position to seek for a mechanical cause of the torsion, for we must have a clear idea of the nature of the result for which we seek a cause. Dealing then first with the nature of the torsion, it is clear, from text-book descriptions, that by torsion of the humerus is meant such a change in the form of the bone as to make the superior articular surface, relatively to the rest of the bone, look medially instead of backwards. Obviously such a change in form could have been brought about by any of the following methods: first, the head of the bone may have been fixed and the lower end rotated medially, or, secondly, the lower end may have been fixed and the head rotated laterally, or, thirdly, there may have been

a combination of both the former methods. With regard to the question of the exact site of the torsion, if a comparison is made between the humerus of a carnivorous Mammal and that of a Man it seems clear that the lower ends and lower two-thirds of the shaft of both bones are very similar. See, for example, Mivart's figure of the anterior aspect of the humerus of a cat (3) and compare it with the figure of the same aspect of a human humerus in Cunningham's *Text-book of Anatomy*. But at the upper end of the shaft, in the region known as the surgical neck, the similarity between the two bones ceases. The figure of the human humerus shows that the upper end of the bicipital groove lies on the antero-lateral side of the bone, and from there the groove winds spirally down to the medial side. The figure of the cat's humerus shows that the upper end of the groove lies on the antero-medial side of the bone, and from there the groove runs straight down. Further, in the cat's humerus the bicipital groove is much wider than it is in the human one. It would appear, therefore, that the torsion has taken place in the region of the surgical neck, and that the twisting of the bone has caused a narrowing of the bicipital groove and has turned its upper end outwards. Thus, in the human humerus, the groove follows a spiral course, as is beautifully shown in the figure of the bone in Cunningham's text-book, though the fact has not been mentioned in the text. The human humerus therefore does show some evidence, in the spiral course of the bicipital groove, of the exact location of the torsion which the bone has undergone.

Moreover, I cannot agree with Duckworth that the course of the musculo-spiral nerve represents torsion in exactly the opposite direction to that which is described as having occurred. For the course of this nerve represents torsion of such a kind that it could have been brought about by fixing the upper end of the bone and rotating its lower end medially, and we have seen that this is one of the ways in which torsion of the humerus, as it exists, could have been produced. It is not intended by this to suggest that the spiral course of the musculo-spiral nerve has any connection with torsion of the humerus as found in the Primates, for the nerve also follows a spiral course in lower animals where torsion of the humerus is not found. But it is necessary, before we seek to explain how the bone has been altered, that we should be quite clear as to the direction in which its lower end has been twisted in relation to its upper end.

So what we want is a mechanism which will tend to rotate the two ends of the bone in opposite directions, the upper end laterally, and the lower end medially, and this mechanism must operate especially in the region of the surgical neck. Fig. 1 shows the two rotations we require. Can we find, in the use of the fore-limb, any peculiarity of the Primates which would produce such a mechanism?

Now in the Primates the fore-limb is used as a tensile organ for supporting the body when suspended from an object overhead in a manner which is quite peculiar to them. The limb when thus used is fully extended and the humerus is therefore in the vertically upright position. Other groups of animals, e.g. the cats, may extend the fore-limb and use it as a tensile organ, but in them the

humerus is not involved, as it is only the part of the limb below the elbow joint that is actually fully extended in line with the body. Besides, many of the Primates use the fore-limb as a tensile organ much more frequently than other animals. So it seems reasonable to look for some connection between this use of the limb and the presence of torsion of the humerus.

In the course of a former paper (2) attention was drawn to some facts about the movements occurring at the shoulder joint in Man which appear to have been generally overlooked up to the present. This paper was especially concerned with the use of the humerus in the vertically upright position and seems to offer a clue as to the mechanism by which the Primate humerus has been modified, and a brief review of its contents may perhaps be allowed, especially as it has only recently been published and its conclusions may not be widely known.

We can carry our arms to the vertically upright position either by flexion, i.e. carrying them forwards and then upwards, or by abduction, i.e. carrying them outwards and then upwards, but no matter which of these ways we may use, the final position of the bones is always exactly the same. This is due to the fact that in carrying the arm upwards by abduction we rotate the humerus laterally round its own long axis to an extent of over 90°, while in carrying it upwards by flexion we rotate the humerus medially to an extent of about 45°. These facts can easily be demonstrated as follows. We can stand in the recognised anatomical position with both arms by the sides and the hands fully supinated so that the palms are directed forwards. Both arms can now be carried to the vertically upright position by abduction while the palms of the hands are kept directed forwards all the time. It may appear that no lateral rotation of the humerus has taken place. But if we note the position of the hands when the arms have reached the vertically upright position, it will be found that they are no longer fully supinated. Supination can now be completed, in which case it will be found that the palms are directed postero-medially. The extent to which we have to rotate the hand in order to complete supination is an index of the amount of lateral rotation that the humerus has undergone during the act of abduction. In other words, as we carry our arms upward by abduction the humerus has rotated laterally, but this rotation of the humerus has been masked by the fact that we have at the same time unconsciously pronated our hands. This demonstration proves further that, owing to our ability to pronate and supinate our hands, we can keep the latter in a fixed position while the humerus is still free to rotate to a considerable extent. This fact will have to be referred to again later on. Another method of proving the rotation of the humerus which occurs during abduction of the arm is to draw an imaginary line through the two epicendyles and to note the position of this line at different stages of abduction. When the arms are in the usual anatomical position by the sides the line will run directly from side to side, that is, transversely. If no rotation of the humerus takes place during abduction, then when the arms have reached the vertically upright stage, the line should again run

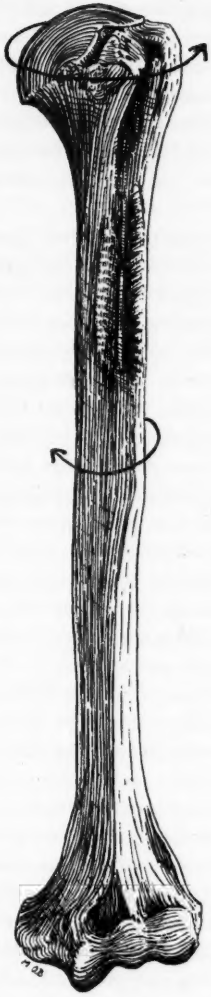

Fig. 1.

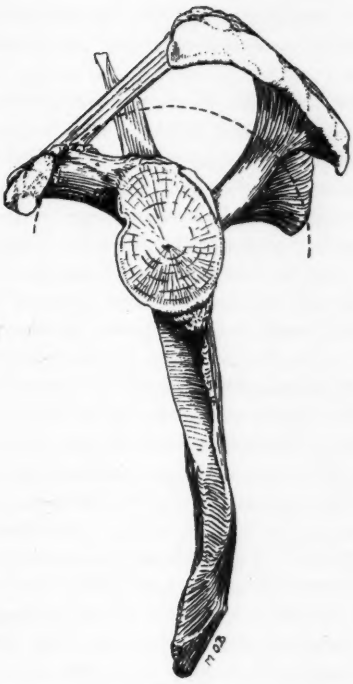

Fig. 2.

Fig. 1. Anterior aspect of humerus. The arrows show the direction of the stresses required to produce torsion of the humerus. Note the spiral course of the bicipital groove.

Fig 2. Lateral aspect of scapula. The broken line is a circle with its centre at the centre of the glenoid cavity. Note that the circle, though touching the coracoid process in front, falls a good deal short of the acromial process behind.

transversely, but the end that had been lateral when the arm was at the side should now be medial. But when we note the position of the end of the line which was lateral at the commencement of the movement we shall find that at the end of the movement it is not medial but has rotated till it is directed postero-laterally. Both these methods of demonstration show that during abduction of the arm the humerus has rotated laterally to an extent of over 90°. It is important in these demonstrations that both arms should be used simultaneously, as otherwise the picture may be obscured by tilting of the thorax.

Similar methods will demonstrate that in carrying the arm upwards by flexion the humerus is rotated medially to an extent of about 45°. Thus if we start again from the recognised anatomical position with the arms at the sides and the palms directed forwards, and carry the arms up by flexion we shall find that, at the completely upright stage, the palms are not directed straight backwards, as they would be if no rotation of the humerus had taken place, but are directed postero-medially. The humerus must have rotated medially about 45°. It should be noted that with the arms in the fully upright position and the hands fully supinated, the palms of the hands are always directed postero-medially no matter how we may have carried our arms to the upright attitude. The descriptions of flexion and abduction of the arm given in the recognised text-books of anatomy fail to notice this feature of the rotation of the humerus, and hence their descriptions of these movements are incomplete and would lead one to infer that the position of the humerus at the end of full abduction is very different from its position at the end of full flexion, whereas it is actually the same.

The lateral rotation of the humerus in abduction of the arm takes place for the most part during the latter half of full abduction, when the arm is carried from the horizontal position to the vertically upright one, but some rotation occurs during the first half of abduction. The slight rotation occurring during the first half appears to be due to the posterior and lower fibres of the deltoid muscle, which take origin from the lower lip of the crest of the spine of the scapula and are inserted into the deltoid eminence on the humerus. Their action is aided by the fact that the deltoid eminence of the humerus is somewhat on the anterior aspect of the bone. But the main part of the lateral rotation, which occurs during the second half of abduction, is due to the greater tuberosity of the humerus coming against the under-surface and outer edge of the arch formed by the acromion and coraco-acromial ligament. This arch, which stretches over the glenoid cavity of the scapula, is not concentric with the glenoid cavity but is nearer to it in front than behind. Hence when the greater tuberosity of the humerus comes against the arch the latter forces the tuberosity to rotate backwards and so rotates the humerus.

It might, at first sight, seem to be more likely that the rotation of the humerus during abduction would be due to one of the muscles passing from the body wall to be inserted into that bone. But consideration of the attachments

of all these muscles practically excludes this possibility. Biceps, triceps and coraco-brachialis arise very close to the head of the humerus and therefore would be little stretched during abduction of the arm, and, in addition, the scapula from which they arise is itself moved to a considerable extent during abduction and this lessens any stretching which they would receive. The trapezius, deltoid and supra-spinatus are contracted during abduction. Other muscles in the neighbourhood are relaxed during this movement, or at least are not actively contracted, and therefore would have little power to rotate the humerus. The three muscles which are contracted cannot, on account of their attachments, be the cause of the rotation, except for the slight amount occurring during the first half of abduction which, as stated above, appears to be mainly due to the posterior fibres of the deltoid. The supra-spinatus may assist this early rotation as it arises somewhat behind the head of the humerus and is inserted directly lateral to it. From their position it might be thought that the infra-spinatus and teres minor are also concerned in the rotation, but, as already stated, these muscles are relaxed during abduction of the arm, and, besides, whatever tendency they may have to rotate the humerus laterally is far outbalanced by the tendency of subscapularis, teres major, pectoralis major and latissimus dorsi to rotate it medially.

Besides, it can be clearly demonstrated, by examining fresh shoulder-joints, that the main part of the lateral rotation of the humerus during abduction of the arm is due to the acromion and coraco-acromial ligament pushing the greater tuberosity of the humerus backwards during the second half of the movement. In ordinary dissecting room subjects the structures surrounding the joint have become too rigid to allow this demonstration to be carried out on them. Fig. 2 is a drawing of the lateral aspect of the scapula showing the position of the acromion and coraco-acromial ligament. The discontinuous line is a circle whose centre corresponds with that of the glenoid cavity, and it may be seen that, while this circle touches the anterior end of the coraco-acromial ligament in front, it falls far short of the acromion behind. This sliding of the greater tuberosity of the humerus under the acromion seems to be the reason for the existence of the extraordinarily large sub-deltoid bursa. Probably also the remarkable laxity of the capsule of the shoulder-joint is due to the allowance which must be made for the very considerable rotation of the humerus in abduction and flexion of the arm. The fact that the anterior end of the arch over the glenoid cavity is composed of ligament perhaps has the advantage that this renders this part of the arch slightly mobile and thus avoids injury to the sub-deltoid bursa if the movement of abduction is carried out very rapidly.

On the other hand, the slight medial rotation of the humerus which occurs during flexion of the arms is, I think, due to stretching of the fibres of the latissimus dorsi, pectoralis major and teres major muscles. All of these are inserted into the anterior aspect of the humerus, and from their attachments it is obvious that they must be greatly stretched when the arm is carried vertically upright. In fact the medial rotation of the humerus would be much greater

but for the fact that it is limited by the arch formed by the acromion and coraco-acromial ligament which will not allow the greater tuberosity of the humerus to pass beneath them. It appears, therefore, that this arch is a very important structure which ensures that when the arm is carried into the vertically upright position, whether by flexion or by abduction, the humerus is rotated laterally round an axis normal to the plane of the glenoid cavity. In abduction the arch directly rotates the humerus round this axis; in flexion the humerus is rotated round this axis by the flexion itself, and the arch simply functions in preventing medial rotation.

If now we use the arm as a tensile organ and hang by it from a beam it is obvious, from the position of the muscles, that the stress due to the body weight will be transmitted through those which have been stretched and not through those which have been contracted. Besides, the structure of the shoulder-joint and the absence of strong ligaments surrounding it point to the fact that it is the muscles which take the greater part of the stress. Of these muscles which are stretched when the arm is carried vertically upright it is evident that the subscapularis will be less affected than the latissimus dorsi, teres major and pectoralis major as it is inserted nearer to the upper end of the bone. But all of these muscles are inserted into the anterior aspect of the humerus, and, if the humerus is rotated laterally as we abduct our arm, they must be twisted round the upper end of the shaft of the bone. Moreover, it is obvious that they must sustain a similar twist if the arm is carried upwards by flexion, for then, even though slight medial rotation of the humerus does occur, the anterior aspect of the bone becomes posterior. When the arm is in the vertically upright position, therefore, these muscles must have undergone a good deal of torsion. These facts can be easily proved. For if we hang from a beam by one arm, our body will always rotate round the arm till the torsion of these muscles is undone. The arm is then in a position of true abduction combined with tilting of the thorax. On account of this tendency of the body, when suspended by one arm, to rotate with the head moving backwards, a gymnast hanging from a beam and moving along it arm over arm must swing his body like a pendulum before he can let go with the rearmost hand. This pendulum swing when he releases the rearmost hand is converted into a rotation of the body with the head moving forwards, which counteracts the tendency of the muscles to rotate it in the opposite direction, and thus he is enabled to bring the free hand round in front.

If, however, the body is suspended by both arms at the same time, or if it is partly suspended by one arm and partly supported by the feet, rotation of the body is prevented, and the twisted muscles must exert a great stress on the humerus tending to rotate it medially. We have seen already that the arch formed by the acromion and coraco-acromial ligament stops the upper end of the bone from medial rotation, so if the lower end is free to rotate medially then the stress exerted by these muscles must produce a strain at the surgical neck of the humerus, the region above the neck being fixed while a force acts on the

region below the neck tending to turn this region medially. As the hands, when grasping a support from which the body is suspended, are in a fixed position, it might be thought that this would fix the lower end of the humerus in like manner as the arch referred to above fixes the upper end of the bone, and so the stress exerted by the muscles would be nullified, both ends of the bone being fixed. But we have already seen, in the demonstration given earlier in this paper, that owing to our ability to pronate and supinate our hand, the latter may be in a fixed attitude and still leave the humerus free to rotate. Provided the hand is not already fully supinated the humerus is free to rotate medially, even though the hand is fixed. This is an important point and can be verified by studying a dissected elbow-joint. If in such a joint we fully supinate the hand and hold it in a fixed position, then we cannot rotate the humerus medially but we can freely rotate it laterally. Or if we fully pronate the hand and fix it in that position, then we cannot rotate the humerus laterally but we can rotate it medially. Now when we use our arms as tensile organs we rarely grasp a support with a fully supinated hand, and therefore we leave the humerus free, as far as the lower end of the bone is concerned, to rotate medially.

Therefore, when we use our arms as tensile organs and hang by them from a support, the stress of the body weight, transmitted through the latissimus dorsi, pectoralis major and teres major muscles must exert a great force on the humerus just below the surgical neck tending to rotate it medially. The subscapularis muscle, as has been pointed out above, is less stretched than the other muscles, and the force it exerts above the surgical neck may be regarded as negligible. On the other hand we have seen that the arch formed by the acromion and coraco-acromial ligament exerts a force on the extreme upper end of the bone, compelling it to rotate laterally if the arm is abducted, and preventing it from rotating medially if the arm is flexed. But the lower end of the humerus is not prevented from rotating medially even if the hand is fixed, unless the hand is fully supinated. Here then, it seems, that we have the two stresses necessary to produce the torsion of the humerus found in the higher Primates, and these stresses arise from a special use of the fore-limb which is peculiar to this group of animals.

Torsion of the humerus is not the only feature of the shoulder-joint region which is peculiar to the Primates. Parallel with it we find other modifications of the pectoral girdle, such as increase of the scapular index and greater development of the acromial process. The former has been shown to be due to the greater range of movement in the shoulder-joint of the Primates as compared with other groups of animals (4). The latter seems to be connected with the increased power of abduction of the arm and consequent greater development of the deltoid muscle found in this group. So it would seem that all the peculiarly Primate modifications of this region are due to increased range of movement, and especially to the ability to abduct the arm and place it in a vertically upright position.

It was stated above that Martin points out that torsion of the humerus is

more marked in female skeletons than in male ones, and in weak skeletons than in strong ones, and that, in the same individual, it is usually more marked in the bone from the left side. These facts suggest that relative weakness of the bone is the most important factor in producing the torsion. If the bone is weak presumably the muscles inserted into it are also weak, and it is these muscles which exert the stress acting below the surgical neck. But it should be remembered that they do not exert this stress in virtue of their power of contraction, for they are stretched when the arm is upright. It is rather by their resistance to over-stretching that they act, and hence they are almost passive organs. Thus relative weakness of the humerus is a more important factor in the production of the torsion than is relative muscular strength.

From what has been written above it is evident that when the arm is upright the subscapularis muscle, though not affected to nearly as great an extent as the latissimus dorsi, pectoralis major and teres major, has been twisted round the upper end of the humerus. When in this position its tendon must be pressed against the anterior edge of the glenoid cavity, and it is suggested that this is the cause of the notch which is found in this locality. The only other explanation of this notch that has been offered is that of Cleland and Mackay (5) who attributed it to the lesser tuberosity of the humerus pressing against the edge of the glenoid cavity when the arm is directed forwards and outwards. For some reason he considered that in this position the arm required a special stability which was gained by this locking mechanism. It is not denied that when the arm is held as described the lesser tuberosity does fit into this notch, but the need for special stability when the arm is in this position is not at all obvious. The explanation of the notch offered in this paper seems to be more reasonable.

SUMMARY

Torsion of the humerus is due to two stresses acting on the bone. One is due to the arch formed by the acromion and coraco-acromial ligament which forces the head of the bone to rotate laterally when the arm is abducted, and prevents the head of the bone from rotating medially when the arm is flexed. The other tends to rotate the shaft medially and is due to the fact that the muscles which take the strain of the body weight, when the limb is used as a tensile organ, are all inserted into the anterior aspect of the bone just below the surgical neck.

The notch on the anterior edge of the glenoid cavity appears to be due to pressure by the tendon of the subscapularis muscle when the arm is carried upwards.

For the illustrations to this paper I am indebted to Miss O'Brien.

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THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE TASMANIAN SKULL

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INTRODUCTION

For the purposes of the present investigation, 91 Tasmanian skulls in private or public collections in the Commonwealth of Australia (including Tasmania) have been examined by one of us (J.W.); and the examinations have been conducted along the lines laid down by the other author, and with his general direction(1). Three skulls examined by R. J. A. Berry and A. W. D. Robertson in 1909(11) have been lost in the meantime, but they are represented by excellent dioptrographic drawings, and measurements, made by these investigators.

To facilitate identification, description, and future reference, the skulls examined have been allotted numbers, following in sequence those already given by Berry and Robertson, making a total of 100, to which has been given the name of the Tasman Series. The collections in which the various skulls are contained are as follows:

Tasman Series

Skull No.	Collection
1–23	Tasmanian Museum, Hobart, Tasmania.
24	Lost.
25–29	Queen Victoria Museum, Launceston, Tasmania.
30, 31	Mersey Bluff Museum, Devonport, Tasmania.
32–38	University of Melbourne, Victoria, Australia (formerly belonged to the late E. O. Cotton, Esq.).
39, 40	Lost.
41–43	Dr W. L. Crowther, Hobart, Tasmania.
44	Dr W. Inglis Clark, Hobart, Tasmania.
45–50	Dr W. L. Crowther, Hobart, Tasmania.
51–55	National Museum, Melbourne, Victoria, Australia.
56, 57	University of Melbourne, Victoria, Australia.
58–60	Institute of Anatomy, Canberra, F.C.T., Australia.
61	Gilbert Rigg, Esq., Melbourne, Victoria, Australia.
62–70	South Australian Museum, Adelaide, South Australia.
71–85	Tasmanian Museum, Hobart, Tasmania.
86–89	Dr W. L. Crowther, Hobart, Tasmania.
90	R. W. Legge, Esq., Cullenswood, Tasmania.
91–96	Queen Victoria Museum, Launceston, Tasmania.
97–99	Tasmanian Museum, Hobart, Tasmania.
100	National Museum, Melbourne.

Nearly all the skulls in the series have been damaged more or less extensively owing to the burial customs of the aborigines, or to lack of care on the part of those unearthing them, or possessing them since being found. The number of skulls, on which observations could be made, is shown in association with each characteristic referred to in this report.

No attempt has been made to determine the sex of these skulls. In the case of the Australian there is generally an obvious difference between male and female, but, while many Tasmanian skulls are clearly masculine or feminine, a large proportion, owing to the remarkable uniformity of size, form, and type exhibited by this race, will probably never be sexed with certainty.

Some four or five skulls in the series may be regarded justifiably as of doubtful authenticity, although they have been accepted by investigators in the past. Reliable historic records reveal the fact that, in the early days of colonisation, Australian aborigines were transported to Tasmania, and Tasmanians to Australia. It is possible that this known interchange across the Bass Strait in precolonial (whaling), and early colonial, days may have introduced some element of doubt as to the actual race to which certain skulls belong. Consequently, an Australoid skull found in Tasmania may be actually that of an Australian, and *vice versa*. It is intended to re-examine the doubtful specimens, and to give the reasons for retaining or discarding them.

MORPHOLOGICAL CHARACTERS

(1) *Cranial form* (95 *crania*)

The Tasmanian does not exhibit such a great difference in cranial form between the male and the female as the Australian: certainly not sufficient to justify separate descriptions.

Norma verticalis. Generally the form is that of a pentagonal ovoid, with pronounced bosses situated far posteriorly on the parietal bones, and a relatively small minimum frontal breadth. The occipital region is broad, and well rounded, but in some specimens it is small in area and prominent. The mediolateral thickness of the zygomatic arch is remarkably small compared with that of the Australian.

Norma lateralis. This view gives the impression of a fairly regularly rounded cranium, possessing good development in the regions about midway between the nasion, bregma, lambda, and opisthion. The lesser degree of prognathism of the Tasmanian compared with the Australian, which has been established craniometrically by all investigators, is visually obvious. Krogman(6) has certainly fallen into error, when he states that "the palate and teeth of the Australian are second only to the Tasmanian in actual and relative proportion."

Campbell(10), who examined the skulls of 138 Australian adults, determined the Australian gnathic index as 104·3. One of the present authors (J.W.) considered that only 86 adult skulls in the Tasman Series were satisfactory for this purpose, as the prosthion was lost or damaged in the majority of skulls and he found the Tasmanian gnathic index to be 103·9.

The characteristic "beetling brow" overshadowing the nasion is slightly more noticeable in the obviously male than in the obviously female skulls.

Norma facialis. Viewed from the front the Tasmanian skull is seen to possess great width across the parietal bosses, and orbits having more than usual depth antero-posteriorly, the facial margins of which form almost true rectangles.

Norma occipitalis. The view from the back reveals the outline to be a slightly irregular pentagon. The parietal bosses are generally clearly defined. In many cases the "depression" of the posterior third of the sagittal suture is more apparent than real, and is due to two well-marked parallel blunt ridges, one on each side of it.

(2) *Cranial asymmetry* (80 *crania*)

Visual determination of this character is at best a crude method. By this test 65 per cent. of these skulls were classified as symmetrical, 6 per cent. as having normal (left occipital prominence), and 29 per cent. reversed (right occipital prominence) asymmetry.

It is anticipated that a method will be devised in the near future whereby this character may be measured quantitatively.

(3) *Sutures* (90 *crania*)

If the varying degrees of complexity of the sutures are described as linear, very simple, simple, complicated, and highly complicated, the general condition found in the Tasmanian was as follows:

Coronal: linear to simple.

Sagittal: simple to complicated.

Lambdoid: complicated to highly complicated.

Only one cranium in the Tasman Series exhibited the metopic suture patent throughout its length, viz. Skull No. 69 (Museum No. P 4), which was described in 1924 by F.W-J.(5).

(4) *Ossa suturarum* (76 *crania*)

These existed in 84 per cent. of the 76 skulls sufficiently well preserved to enable the sutures to be seen. The total number of ossicles in the 64 skulls possessing them was 220, an average of over three each, one skull having as many as 14, all in the lambdoid suture. In the total of 64 skulls with ossicles, 56 per cent. had them bilaterally, and 38 per cent. unilaterally, in the lambdoid; 19 per cent. had them at lambda; 11 per cent. in the occipito-mastoid suture; and 47 per cent. at asterion.

Of the total of 220 ossicles, 202 were observed in the lambdoid suture, 46 per cent. of which were on the right, 44 per cent. on the left and 10 per cent. at lambda.

Four skulls exhibited one ossicle, and one skull four ossicles in the sagittal suture, while one skull had one in the coronal suture.

Only one skull possessed an os interparietale.

(5) *Pterion* (59 *crania with both sides intact*, 10 *crania with one side missing*)

The normal alisphenoid-parietal contact was regarded as wide, when 10 mm. or longer, as usual when between 5 and 10 mm., and as narrow when 5 mm. or less.

The pterion was of normal contact, bilaterally, and of usual size in 34 per cent., wide in 12 per cent., and narrow in 10 per cent. of the skulls.

Its site was occupied by an epipteric bone on one side, but it was of normal contact, and usual size on the other, in 10 per cent., and normal and narrow in 10 per cent. Epipteric bones were found to occupy completely the pterion bilaterally in 8 per cent. An epipteric bone unilaterally, accompanying a normal, large, contact was seen in three skulls, while two were found to have the pithecoid contact (temporo-frontal) bilaterally. Of two skulls having normal contact bilaterally, one had the pterion of usual size on one side, and wide on the other, while the second exhibited the usual size on one side, and narrow contact on the other.

Each of the following conditions was observed once:

(*a*) The pterion on one side was formed partly by normal contact, and partly by an epipteric; while, on the other side, it was completely occupied by an epipteric.

(*b*) The partly normal and partly epipteric pterion on one side, and a normal, wide contact on the other.

The pterion of the side remaining in the 10 skulls, in which one side was missing, was found to be as follows in the number of skulls indicated:

(*a*) Normal contact, of usual size in two skulls.

(*b*) Normal contact, and narrow in three skulls.

(*c*) Normal contact, and wide in one skull.

(*d*) By epipteric in three skulls.

(*e*) Pithecoid contact in one skull.

(6) *Epipteric bones* (72 *crania*)

These were found either bilaterally, or unilaterally, in 37 per cent. of the skulls, the bilateral cases being 10 per cent. In 6 per cent. an epipteric was observed on the right only, and in 21 per cent. on the left only.

One skull had two on the right side, and none on the left.

(7) *Supra-orbital foramina, notches or grooves* (79 *crania*)

Grooves, bilaterally, some being very shallow, were found in 38 per cent. of the skulls, and notches bilaterally in 21 per cent. A notch on one side, and a foramen on the other, were present in 8 per cent.; a groove and an accessory foramen, bilaterally, in 5 per cent.; a notch and an accessory foramen, bilaterally, in 5 per cent.; and a notch, bilaterally, with an accessory foramen unilaterally in 5 per cent.

Each of the following conditions occurred twice only in the series: (*a*) a foramen bilaterally, (*b*) a foramen on one side, and a notch with an accessory foramen on the other, (*c*) a notch on one side, and a groove on the other, and (*d*) a notch and accessory foramen on one side, and a groove and accessory foramen on the other. Each of the following conditions occurred only once in the series: (*a*) a groove bilaterally, and an accessory foramen unilaterally; (*b*) a foramen and an accessory foramen, bilaterally; (*c*) a groove bilaterally, one with one accessory foramen and the other with two; (*d*) a notch on one side, and no indentation or foramen on the other; (*e*) a foramen on one side, and a groove and accessory foramen on the other; and (*f*) a foramen bilaterally, one accompanied by an accessory foramen.

Accessory foramina bilaterally were observed in 14 per cent. and unilaterally in 10 per cent.

(8) *Anterior ethmoid canal* (*40 crania with both sides intact and seven having one side missing*)

It was found in the suture, bilaterally, in 85 per cent. of the skulls; in the frontal bone, bilaterally, in 8 per cent.; and in the frontal bone on one side, and in the suture on the other, in 5 per cent. In one case it was present in the frontal bone, but confluent with the suture, bilaterally.

In the seven skulls in which the wall of the orbit had been lost on one side, the canal on the other side was in the suture.

It was not located in the lamina perpendicularis of the ethmoid in any skull examined.

(9) *Sutures of the inner wall of the orbit*

No abnormal arrangement of these sutures was observed in any skull in the series.

(10) *Spheno-maxillary fissure* (*59 crania*)

Using the terms linear, narrow, moderate, and wide to describe this character, 36 per cent. were classified as narrow, 47 per cent. as moderate, and 17 per cent. as wide.

(11) *Form of the orbit*

The form of the Tasmanian orbit approaches more closely to a rectangle than that of the Australian, or of most other races. In a large majority of cases there is only slight obliquity of the longitudinal axes, while in many skulls, generally the obviously masculine, there is no obliquity apparent, but in the obviously feminine the obliquity is more evident.

The "beetling over" of the massive supra-orbital region is too well known to need reference here.

There is one feature of the Tasmanian orbit which is not clearly shown in dioptrographic drawings, but which serves as a useful distinction between Australian and Tasmanian skulls. It is the inferior margin. In the skulls of both races it is common to find the superior margins straight for almost their

whole length, and with little, or no, obliquity. In the Australian skull the inferior margin inclines upwards at each end, and more particularly at the medial end. In addition, the obliquity of the inferior margin is generally greater than that of the superior margin. In the Tasmanian skull, the inferior margin is straight over a larger part of its length, and the obliquity of the inferior margin is generally equal to, or only slightly greater than, that of the superior margin. The inferior margin is usually fairly thick and well rounded, while in the Australian, it is generally thinner, a condition which may be due to the canine fossa being deeper, and extending to a higher level than in the Tasmanian.

(12) *Infra-orbital foramen* (*59 crania with both maxillae and nine with one each*)

The conditions found in this region are so varied that analysis is unavoidably cumbersome.

A normal foramen (for want of a better term) was present, bilaterally, in 27 per cent., and a normal foramen with an independent suture to the inferior orbital margin, bilaterally, in 25 per cent. of the skulls.

The number of times the following conditions were observed in the series is indicated:

Four times.

A normal foramen and suture on one side, with a normal and an accessory foramen, both on the same suture from the inferior orbital margin, on the other.

Three times.

A normal foramen on one side, and a normal and an accessory foramen on the other. A normal foramen with a suture from the inferior orbital margin on one side, and a normal foramen on the other.

Twice.

A normal and an accessory foramen bilaterally.

A normal foramen and an incomplete suture bilaterally.

A normal and an accessory foramen, both on the same suture, on one side, and a normal foramen with its suture, and an accessory foramen medial to the suture on the other.

Once.

A normal foramen on one side, and a normal and two accessory foramina on the other.

Bilaterally, a normal foramen and an accessory foramen, the latter having an independent suture.

A normal and an accessory foramen both on one suture, on one side, and a normal and an accessory foramen each having a separate suture on the other.

A normal and an accessory foramen on the same incomplete suture on one side, with a normal and two accessory foramina on the other.

A normal and an accessory foramen on the same incomplete suture on one side, and a normal and one accessory foramen on the other.

A normal and an accessory foramen on the same suture on one side, and a normal and an accessory foramen, the latter having an independent suture, on the other.

A normal and two accessory foramina all on one incomplete suture on the one side, and a normal foramen with an incomplete suture on the other.

A normal foramen and a suture on one side were accompanied once, with each of the following conditions:

(*a*) a normal and an accessory foramen;

(*b*) a normal foramen and its suture with an accessory foramen medial to the suture;

(*c*) a normal foramen and an accessory foramen, the latter having an independent suture;

(*d*) a normal and an accessory foramen, and an incomplete suture;

(*e*) a normal foramen and an incomplete suture.

Of six skulls with the left maxilla missing, all had a normal foramen on the right, a suture accompanying it in one instance. Of three with the right maxilla missing, one had a normal foramen, the second a normal and an accessory foramen, and the third a normal foramen and a suture on the left.

No attempt has been made to classify the orbital terminations of the sutures running from the various foramina to the inferior orbital margins.

One accessory foramen was present bilaterally in 15 per cent. and unilaterally in 19 per cent.; two of them unilaterally in 3 per cent., and two on one side and one on the other was seen once.

A complete, or an incomplete, suture to the infra-orbital margin was present bilaterally in 52 per cent., and unilaterally in 10 per cent. One skull had one suture on one side, and two on the other, one of the latter being connected with the normal, and the other with an accessory foramen.

(13) *Form of the jugal*

No instance of subdivision of the malar bone was observed.

Compared with the size of the whole skull, the bones constituting the zygomatic arch of the Tasmanian are of slight construction, being particularly thin medio-laterally.

(14) *The nasal bones* (71 *crania*)

About the inferior half of nearly every nasal bone examined had been lost through damage; consequently, reliable measurements of their length could not be obtained.

The Tasmanian nasal bones seem to be narrower at the constriction near their superior extremities than the Australian. They were regarded as of usual width when the minimum width across both bones at the constriction was 7 mm., and as narrow, or wide, when less than, or greater than, this measurement respectively.

They were found to be normal in width across both bones, and approximately symmetrical in 38 per cent.; normal and asymmetrical in 20 per cent.; narrow and symmetrical in 15 per cent.; narrow and asymmetrical in 7 per cent.; wide and symmetrical in 14 per cent.; and wide and asymmetrical in 6 per cent. of the skulls.

Asymmetry in the width of the two bones was found in 33 per cent. of the skulls, the right being the wider in 18 per cent. and the narrower in 15 per cent.

The internasal suture was synostosed completely in 8 per cent. and partly in 6 per cent.

An unusual variation of the superior part of the internasal suture was seen in approximately five skulls. In them, the suture started at a point to the right or left of the median line, proceeded inferiorly for 2–3 mm., and then turned towards the opposite side, and, after crossing the median line and turning inferiorly again, it curved towards the median line, and followed a straight course inferiorly. The upper part of the suture thus appeared somewhat like the form of the letter "S" lying sideways.

In one skull it was found that the whole length of the frontonasal suture was formed by the frontal border of the right bone alone. The internasal suture began from the maxillary border of the left bone, about 2 mm. from the frontal border, and was directed almost straight to the median line.

(15) *The narial aperture*

This was pyriform in shape in almost all skulls possessing the facial part, its average width for 64 skulls being 26·8 mm. In two or three skulls, the authenticity of which was regarded as doubtful by the present authors, it was "almost parallel-sided."

In a large majority of the skulls the upper part of the lateral margin was single and sharp, but in only one or two was the inferior border not "guttered." In a few instances the whole of the lateral margin was double. The double inferior margins were generally blunt and smooth.

(16) *The nasal septum*

The nasal septum was observed to be almost complete in only three skulls, while about half of it was present in five. In the former it was very slightly deflected towards the right in two skulls, and was perpendicular in the third, while in all the latter the part remaining was perpendicular.

(17) *Foramen ovale* (62 *crania undamaged and* 10 *in which the bones on one side have been lost*)

The average size of this foramen was found to be 5–6 mm. long, by 3 mm. wide. It was found complete, and of average size, bilaterally, in 52 per cent. of the undamaged skulls; complete and small in 15 per cent.; complete and round in 6 per cent., and complete and large in 5 per cent.

It was complete and of average size, unilaterally, with the following conditions on the other side: (*a*) incomplete in 6 per cent, (*b*) complete and round in 3 per cent., and (*c*) confluent with the foramen spinosum in two skulls.

It was incomplete bilaterally, and confluent with the foramen spinosum bilaterally, once each in the series.

Incomplete foramina were present in 8 per cent. of the 72 skulls.

Four skulls in the series had the following unusual conditions:

(*a*) On the right side there was a condition similar to that shown in fig. 6 of (1). On the left, the foramen ovale was incomplete, and the ridge from the lamina lateralis pterygoidei terminated near its anterior end. Lateral to the foramen was another ridge, which arose close to the spheno-maxillary fissure, and which was pierced by a short transverse canal near to the foramen ovale, the orifices of the canal opening on the medial and lateral aspects of the ridge respectively.

(*b*) On the right side, the foramen was complete, and the condition was somewhat similar to that shown in (1) (fig. 10) except that the medial bar arose between the two pterygoid plates, and was not a continuation of either. On the left the arrangement was similar, except that the foramen ovale was incomplete medially.

(*c*) Near the posterior part of the lateral margin of each foramen ovale there was a small foramen confluent with it.

(*d*) The condition on each side was similar to that on the right of (*a*), except that, on the right, there was a groove instead of a canal through the ridge.

The conditions found in the 10 skulls, in which one side of the base had been lost through damage, are as follows:

(*a*) Complete, and of average size, four skulls.
(*b*) Confluent with the foramen spinosum, two skulls.
(*c*) Complete, and round, two skulls.
(*d*) Complete, average size, and lateral to "pterygospinous bar," one skull.
(*e*) Incomplete medially, one skull.

(18) *The foramen of Vesalius* (60 *crania, both sides intact, and two crania, one side missing*)

This foramen was present and complete, bilaterally, in 40 per cent.; present and complete, unilaterally, in 22 per cent.; and absent, bilaterally, in 37 per cent.

It was present, but incomplete, bilaterally, in one skull.

Of the two in which one side is missing, the remaining side was observed to have the foramen present, and complete in one, but absent in the other.

(19) *Foramen spinosum* (60 *crania with both sides intact and nine with one side missing*)

Only the external orifice of the "canalis spinosus" was examined.

In 38 per cent. of the 60 skulls it was bilaterally complete, and in 33 per cent. unilaterally complete.

It was incomplete, bilaterally, in 22 per cent.

Twice it was found bilaterally confluent with the foramen ovale; once complete, and situated high on the spina angularis, bilaterally, and once complete, and situated high on the spina, unilaterally. It was present once bilaterally, and twice unilaterally, lateral to the terminal ridge from the lamina lateralis pterygoidei.

Each of the following conditions was observed once:

(*a*) Bilaterally double orifices, one on each side of the ridge from the spina, each lateral one being complete, and the medial incomplete.

(*b*) It was complete on one side, but incomplete medially on the other, and situated high on the spina.

(*c*) It was complete on each side, but on the right it had two orifices, one medial and the other lateral to the terminal ridge of the lamina lateralis pterygoidei.

(*d*) Incomplete, medially, on one side, and confluent with the foramen ovale on the other.

Of the nine skulls, one side of the base of which has been lost through damage, four had complete foramina, in normal position on the remaining side; two had an incomplete foramen each; one had the foramen incomplete medially and confluent with the foramen ovale; one presented a complete foramen with two orifices, one on each side of a ridge, and the last an incomplete foramen on the spina.

(20) *Spina angularis sphenoidei* (*57 crania with both sides intact, eight crania, one side missing*)

The most noteworthy features were observed to be its shortness, and its generally typical shape, resembling, somewhat, the end of a very blunt arrow-head. This type of spina was found to be short, and blunt, bilaterally, in 53 per cent., and long, and sharp, bilaterally, in 9 per cent. Of three skulls having this type, short and blunt on one side, one had a similar type but short, and sharp, on the other, while two had a short blunt cone on the other.

It was a conical spine, short and blunt, bilaterally, in 18 per cent., and long and sharp, bilaterally, in 5 per cent.

In two skulls in the series the spina on each side resembled a rose thorn in shape, and was curved upwards.

Of the eight skulls in which one side had been lost, the spina on the remaining side was of the short, blunt, arrow-head type in four; of similar type but long, in one; conical, and short in two, and conical and long in one.

Each of the following conditions was observed once in the series: (*a*) conical and short on one side, and conical and long on the other; (*b*) bilaterally the abrupt termination of a ridge; (*c*) a short, blunt arrow-head, and bifid, bilaterally.

(21) *Laminae pterygoidei* (*54 crania, both sides intact, and five crania, one side missing*)

The laminae had been lost by damage in so many skulls in the series, that a reliable comparison of their widths could not be obtained.

The attached margin of the lateral lamina faded away as a ridge close to the anterior margin of the foramen ovale, bilaterally, in 70 per cent. of the skulls. In 9 per cent. it faded medially, and in 9 per cent. laterally to the foramen. It terminated, unilaterally, near the anterior end of the foramen ovale, and on the other side lateral to the foramen in 6 per cent., and medial to it in 6 per cent.

In the five skulls, in which one side was missing, the remaining side in each of them exhibited the normal condition of the ridge from the lateral lamina terminating anterior to the foramen.

Only once was a complete pterygo-spinuous bar observed, and it passed medially to the foramen ovale.

(22) *The jugular fossa and foramen* (*53 crania*)

In 68 per cent. of these skulls the foramen on the right was larger than that on the left, in many cases being twice as large. Equality between the two sides was seen in 23 per cent., while 9 per cent. exhibited the left foramen larger than the right.

(23) *The tympanic* (*67 crania, both sides intact, one cranium, one side missing*)

In 67 per cent. of these skulls the conditions found were classified as normal, bilaterally, while the part of this bone forming the floor of the mouth of the external auditory meatus was regarded as thick, bilaterally, in 18 per cent., and thin, bilaterally, in 10 per cent. Its margins at the meatus were much rougher than usual in 9 per cent. Exostoses in the external meatus were observed in 9 per cent. of the skulls.

In 6 per cent. the external auditory meatus was much larger in its supero-inferior dimension, and smaller in its antero-posterior than usual. A rough ridge was noted on its lower surface in 6 per cent. of the skulls, in some cases being low and incomplete, while in others it was higher than the spina angularis sphenoidei, and almost continuous with it.

In the skull in which one tympanic had been lost, the remaining one exhibited normal conditions. The inferior margin of the mouth of the external auditory meatus was deeply notched, bilaterally, in one skull.

(24) *Foramen of Huschke*

This was not seen in any skull.

(25) *Styloid process* (*36 crania with both sides intact, three crania with one side missing*)

It varied bilaterally from small in cross-section, and short in length, to being rudimentary in 69 per cent.

In 8 per cent. it was absent, bilaterally, and very thick, bilaterally, in 8 per cent. Two skulls were classified as having moderately thick processes.

It was observed to be absent, unilaterally, in three skulls, one of which has a moderately thick process on the other side, the second a small fine process, and the third a rudimentary process.

Of the three skulls, one side of which had been lost through damage, one presented on the remaining side a styloid process that was small in section and short in length; the second a rudimentary process; and the third a long but thin process.

The vaginal process was small, and slight, in almost all the skulls in which it was observable, being well developed in only six skulls in the series.

(26) *The posterior condyloid foramen* (*58 crania*)

This foramen was present, bilaterally, in 43 per cent.; unilaterally, in 28 per cent.; and absent bilaterally in 29 per cent. of these skulls.

One additional characteristic, the pre-maxillo-maxillary suture is considered worthy of inclusion.

The pre-maxillo-maxillary suture (*45 crania*)

Unfortunately, the palate in the majority of skulls examined had been lost, or damaged by incineration, or some other cause. In only 45 skulls was its anterior part so well preserved that it was possible to make a reliable determination of whether the pre-maxillo-maxillary suture was patent or not. In 42 of them it was noticeable with the naked eye, or with the use of a magnifying glass, and it therefore occurred in 93 per cent. of these cases.

The generosity of the Council of the University of Melbourne in granting a research scholarship to one author (J.W.) enabled the examination of the skulls referred to in this report to be made.

Our thanks are due to all in Australia and Tasmania who possess private collections, or who have charge of public collections of the skeletal remains of the Tasmanian, for their readiness to grant access to the material examined.

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MEASUREMENT OF THE CHINESE ORBIT

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It is a remarkable fact that although the complete measurements of the bony orbit have been recorded for many races, there has hitherto been no exhaustive investigation of the peculiar characteristics of the orbit of the Chinese. This is the more remarkable since the facial peculiarities of the Chinese, especially with regard to the orbit, have long attracted the attention of physical anthropologists.

It is well known to ophthalmic surgeons practising in China that the standards as laid down by European authorities are not strictly applicable in the case of the Chinese. It is, therefore, a matter of some importance that full measurements carried out upon a satisfactory series of skulls should be available. In the present investigation the orbits of 90 skulls of known age and sex have been measured. The skulls belong to the collection of the Department of Anatomy and are those of Northern Chinese ranging in age from 19 to 65 years and all the crania included in the series are those of males. The measurements taken were the orbital height, orbital width, orbital depth and orbital volume. The figures for the right and left sides have been combined.

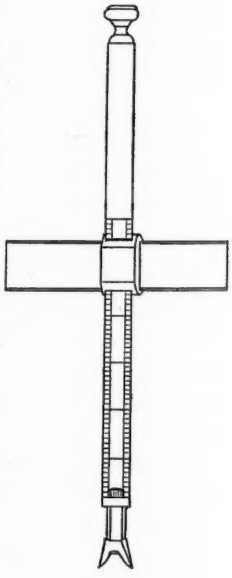

Fig. 1.

The height was taken along the line running parallel to the lateral and medial margins at the mid-point of the horizontal diameter. Since the orbital width has been taken in so many different ways by various workers, it has been thought best to record the three most usual measurements: (*a*) from the maxillary-frontal point, (*b*) from the dacryon point, where the upper end of the lacrimo-maxillary suture meets the frontal bone, and (*c*) from the lacrimal point, where the upper end of the lacrimal crest meets the frontal bone. Measurements from these three points upon the nasal aspect of the orbit have been taken to the outer wall along a line parallel to the upper and lower orbital margins.

The measurements of height and width were taken by using a pair of fine

dividers and reading off the separation of their points upon a steel millimeter measure.

Orbital depth was measured by means of an instrument specially designed and constructed by me for the purpose (see fig. 1). The terminal fork of the instrument is so constructed that it is permitted to rotate in the axis of the measuring rod. The forked end is inserted astride the bar of bone separating the optic foramen from the superior orbital fissure, and the cross bar of the instrument is then brought into apposition with the orbital margins at the points used in measuring the vertical diameter of the orbit. A direct reading is then taken on the measuring rod of the instrument. The volume of the orbital cavity was taken by sealing all the orbital openings with plasticine and then carefully filling the cavity with fine sand. By means of slight movements the level of the sand was brought to the level of the orbital margins. The volume of the sand was then directly measured by means of a graduated glass cylinder.

The following table gives the results of these investigations.

Height in mm.	Mean	=	36·7
	Standard deviation	= ±	2·2
	Coefficient of variation	=	5·9
Width (from maxillary frontal point)	Mean	=	42·7
	Standard deviation	= ±	1·9
	Coefficient of variation	=	4·5
Width (from dacryon point)	Mean	=	39·8
	Standard deviation	= ±	1·9
	Coefficient of variation	=	4·7
Width (from lacrimal point)	Mean	=	36·6
	Standard deviation	= ±	1·7
	Coefficient of variation	=	4·6
Orbital depth	Mean	=	47·9
	Standard deviation	= ±	2·7
	Coefficient of variation	=	5·6
Orbital volume	Mean	=	29·3
	Standard deviation	= ±	2·5
	Coefficient of variation	=	8·5
Orbital index (width from maxillary point)	Mean	=	86·6
	Standard deviation	= ±	4·9
	Coefficient of variation	=	5·7
Orbital index (width from dacryon point)	Mean	=	93·0
	Standard deviation	= ±	5·5
	Coefficient of variation	=	5·9
Orbital index (width from lacrimal point)	Mean	=	100·8
	Standard deviation	= ±	6·2
	Coefficient of variation	=	6·1

SUMMARY AND CONCLUSION

In spite of the narrowness of the palpebral fissure of the Chinese eye, the orbital measurements recorded here are in no way smaller than those of other races: on the contrary the vertical diameter of the Chinese orbit is much greater than that recorded for any other race. It therefore follows that the orbital index of the Chinese is unusually high. Although, owing to the

difference in the methods of measurement, the figures for the orbital depth in my series are not strictly comparable with those given by other authors, it is probable that the depth of the Chinese orbit exceeds that of the European as quoted by Whitnall.

The orbital volume of 29·5 c.c. is however remarkably similar to that of the European orbit recorded by Weiss (29·74 c.c., quoted by Whitnall, p. 85).

Despite the fact that the height and depth of the Chinese orbit exceed the same diameters of the European, whilst the width is practically the same in both cases, the volume of the Chinese orbit would appear to be no greater than that of the European. Probably the reason for this is the characteristic encroachment of the mesial wall into the orbital cavity of the Chinese.

The writer wishes to take this opportunity of thanking Prof. A. Pillat for his valuable suggestions which have made the writing of this paper possible.

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PATTERNS OF THE AORTIC ARCH IN AMERICAN WHITE AND NEGRO STOCKS, WITH COMPARATIVE NOTES ON CERTAIN OTHER MAMMALS

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The present report treats in a statistical way the varieties of branches associated with the aortic arch as found in dissecting-room material of this laboratory between the years 1925 and 1932. This material comprises 314 specimens, distributed as follows according to race and sex: white males 98, white females 13, total whites 111; negro males 138, negro females 65, total negroes 203. These totals include the following numbers of infants: 3 white males, 8 white females, 13 negro males, 9 negro females. For completeness of the record entry is made of the distribution of male and female adults and infants according to the various patterns, even though only gross totals are required for expressing incidence as to race.

In addition to this human material, a large number of aortic arches from other Mammals has been collected and dissected by one of us (C.D.). This comparative material is in the main from Primates, but also includes samples from other Mammals, the largest series being 42 specimens from the domestic cat. Separate reports will doubtless be made as this material accumulates, but here brief notes are introduced where comparisons with the human patterns are apposite.

With few exceptions the present report offers no new or extreme anomalies of the human aortic stems. Most of the patterns in this series have been figured by Tiedemann (1822), Bourgery (1836), Quain (1844), Dubrueil (1847), Le Double (1901) or other commentators, whose works depict many bizarre arrangements of aortic arches and branches, in part cited from sources so remote as to be now inaccessible. The excellent review of aortic patterns available in the work of Poynter (1916) renders the historical treatment of this subject unnecessary here. The interest of the present report then centres neither on a comprehensive survey of the subject nor on the novelty of the specimens described, but rather on the comparative frequency of normal and diverse patterns of aortic stems in the American white and negro races, thus bearing on the important question of racial variability.

For each of the patterns described below the relative frequencies will be

compared, wherever possible, with results obtained by other workers in this field. A previous report on aortic stems (De Garis (1923), hereafter designated Report I) has in some recent literature been misquoted for reasons largely inherent in the undue brevity of the report itself. Thus the failure to express pattern frequency in some customary fashion, i.e. per centum or per mille, has doubtless led to misquotation.

Since the records of Report I are still on file, it seems desirable to canvass them again and express their data according to the standards of the present report. Among these previous records it is found that 4 white males, 9 negro males and 1 negro female had an arrangement of aortic stems now accounted outside the normal, namely that in which the anonyma and carotis communis sinistra arise by a common root, as distinguished from a common trunk (see pattern B, figs. 1 B, 2 and 4). Since the adjusted frequencies of Report I are based solely on graphic records and notes, wherein no account is taken of the exits of stems viewed from the interior of the aorta, it is altogether probable that these frequencies are still far too low. Further, in keeping with the present standards, deduction from the number of normal patterns should include cases of the thyreoidea ima arising from the anonyma, this variant having been accurately set forth in Report I as present in 1 white female, 3 negro females and 1 negro male. The foregoing amendments to Report I are effective in the citations per centum given below.

PATTERNS AND INCIDENCE

The patterns of aortic branches are, with some exceptions, described and figured here in the order of their frequency. Arbitrarily, but as a matter of record, cases of the thyreoidea ima arising from the anonyma are accounted among anomalies associated with the aortic arch, as are cases of the vertebralis sinistra arising from the subclavia sinistra very near the arch. In the several line-drawings of patterns (fig. 1) a conventionalised stencil of the aortic arch is employed throughout, since attention is here directed solely to the arrangement and diversity of the branches. Photographs of certain specimens acquired during the past two years are shown in Plates I and II (figs. 2–12), where again no attempt is made to indicate the relative dimensions of the specimens.

Pattern A

The usual text-book sequence of aortic branches (pattern A, fig. 1 A) is the one most frequently found both in the whites and in the negroes of our series. Therefore it is taken as the normal from which variability is measured. No special comment is required as to the general disposition of this pattern. However, it should be noted that here, as in other patterns, the branches show much diversity as to spacing and occasional diversity as to alignment. The prevailing tendency among negroes is for the anonyma and carotis com-

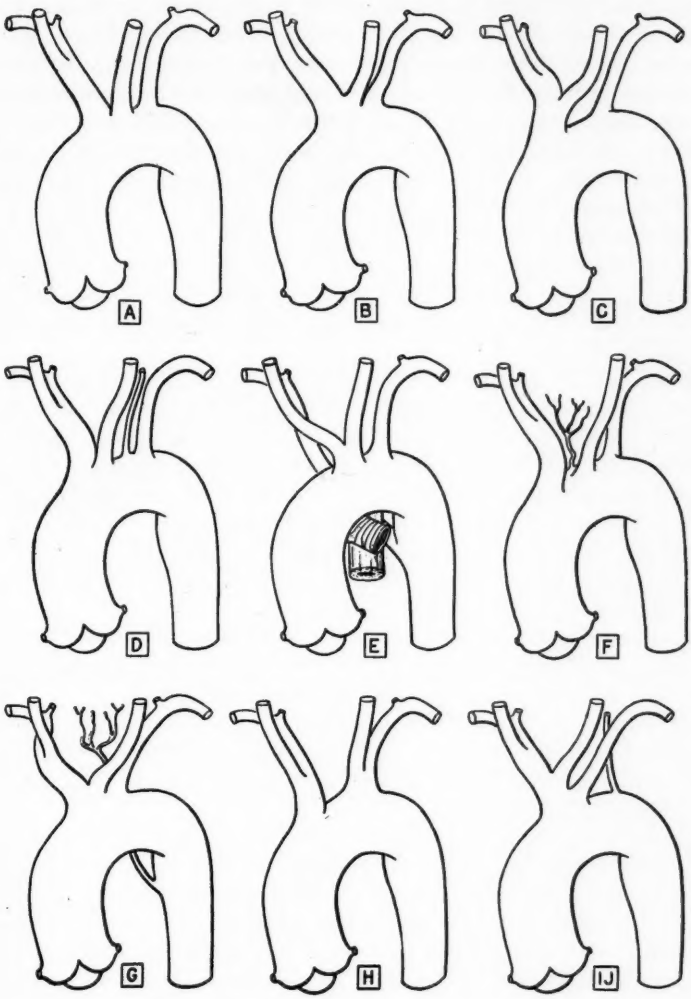

Fig. 1. Diagrammatic ventral views of aortic patterns. A, the normal pattern. B, radix communis for anonyma and carotis communis sinistra. C, truncus communis for anonyma and carotis communis sinistra. D, vertebralis sinistra as aortic stem between carotis communis sinistra and subclavia sinistra. E, subclavia dextra as last branch of aortic arch. F, thyreoidea ima as aortic stem between anonyma and carotis communis sinistra. G, thyreoidea inferior as branch of descending aorta. H, anonyma dextra and sinistra. IJ, radix communis—truncus communis for all great stems of aorta, and vertebralis sinistra as last branch of aortic arch.

munis sinistra to arise close together from the arch, while the subclavia sinistra has a variable placement to the left (66/97 negroes or 68 per cent.). Among whites the carotis communis sinistra usually arises about midway between anonyma and subclavia sinistra (62/86 whites or 72 per cent.). In 22 cases (19 negroes, 3 whites) the three stems, though separate, emerge close together from the right extremity of the arch, thus continuing the ascending aorta and leaving the highest part of the arch without branches. In 6 of these cases (5 negroes, 1 white) and in 4 others (negroes) the aortic branches are grossly out of alignment. Here the anonyma is initially inclined somewhat to the left; the carotis communis sinistra may be in front as well as to the left of the anonyma and has a very oblique placement directed to the left; the subclavia sinistra lies variously behind and to the left of the carotis communis sinistra. Figs. 4 and 5 exemplify this right-sided clumping and malalignment as of pattern B.

In 20 cases (14 negroes, 6 whites) the two left stems, though distinctly separate, arise close together and usually more or less removed from the anonyma toward the left extremity of the arch. In 3 cases (1 white male, 1 negro male, 1 negro female), the anonyma is very short, the subclavia dextra and carotis communis dextra failing the status of separate aortic stems by 1–2 cm.* These various irregularities of spacing and alignment appear to offer no significant basis for classification, though it is obvious that they are much more frequent among negroes than among whites. Adachi (1914) has noted diverse spacing of aortic stems in the Japanese.

Incidence of pattern A: 86 *whites* (77·4 ± 3·97 per cent.) (males: 78 adults, 2 infants; females: 2 adults, 4 infants); 97 *negroes* (47·7 ± 3·50 per cent.) (males: 62 adults, 7 infants; females: 25 adults, 3 infants).

Incidence of pattern A from the literature, per centum: English—Quain (1844) 84, Thomson (1893) 82·4; Japanese—Adachi (1928) 83·3; Negro—Loth (1912) 78; American Negro—Report I (1923) (amended) 73·5; American White—Report I (1923) 84·6.

Among our mammalian material the normal human sequence, pattern A, is found in the following numbers of specimens: domestic cat (*Felis domestica*) 1, spider monkey (*Ateles ater*) 1, capuchin monkey (*Cebus malitiosus*) 1, Bengal macaque (*Pithecus rhesus*) 1, chimpanzee (*Pan* sp.?) 3, the tarsiers (*Tarsius philippinensis*) 1 and (*Tarsius saltator*) 1. In our two specimens of *Tarsius* the aortic arch is conspicuously lower and broader than any we have seen in Man, the two left stems emerging close together and diverging widely from

* The pattern of the four great stems arising separately and in sequence from the aorta has been found by Tiedemann (1822) in nine reports from the European literature. However, no record of such a pattern appears in the large series of Thomson (1893) and Adachi (1928). In a negro specimen of Report I (1923) there was the right-to-left sequence: subclavia dextra—truncus bicaroticus—subclavia sinistra. No other separate subclavia dextra has been found by us, except as arising anomalously from the left extremity of the arch (here pattern E). Of interest in this connection are the report by Vallois (1929) and the book by Weinert (1932).

the anonyma. Wood Jones (1929 and previously) regards the human sequence of aortic stems in *Tarsius* as an item supporting his view that this genus is more nearly related to Man than are the other Primates. Two facts would seem to relieve this argument of some significance, namely: (1) the human sequence of aortic stems occurs at times in Primates other than *Tarsius*, and in various other Mammals (see Parsons, 1902); (2) the prevailing mammalian pattern of truncus communis for anonyma and carotis communis sinistra occurs as one of the frequent variants in Man.

Pattern B

Next in order of frequency is pattern B, characterised by a common root of origin for anonyma and carotis communis sinistra (figs. 1 B, 2 and 4). This common root is easily recognised from the exterior, yet if the aortic arch be incised along its concavity and turned inside out, the exit of the common root is most strikingly demonstrated (see figs. 3 and 5).

Frequent and obvious as this pattern is, it has not been accounted separately in the literature. Thomson (1893) evidently includes it in the pattern of the common trunk for anonyma and carotis communis sinistra, since he remarks that this common trunk may vary in length from $1\frac{1}{4}$ in. to zero. Now a common trunk of zero length is manifestly not a common trunk at all; it is merely a common root, or, exemplified as a geometric model, it is the common intersection of two cylinders, the anonyma and carotis communis sinistra, with a third, the aorta. This distinctive configuration of pattern B we propose to call *radix communis*. Developmentally and in point of frequence the radix communis stands intermediate between the disparate arrangement of pattern A and the *truncus communis* of pattern C.

Not infrequently the radix communis and the origin of the subclavia sinistra, though separate, are crowded together at the right extremity of the arch, and occasionally one of the left stems is much out of alignment. Figs. 4 and 5 are of a specimen showing this right-sided crowding with forward displacement of the carotis communis sinistra.

Incidence of pattern B: 9 *whites* (8·1 ± 2·59 per cent.) (males: 4 adults, 1 infant; females: 1 adult, 3 infants); 51 *negroes* (25·1 ± 3·03 per cent.) (males: 30 adults, 3 infants; females: 17 adults, 1 infant). Report I (1923) amended: 4 whites (7·7 ± 3·69 per cent.); 10 negroes (11·5 ± 3·42 per cent.).

Among our mammalian material the radix communis is found in the following: *Felis domestica* 2, *Pithecus rhesus* 1, squirrel monkey (*Saimiri sciureus*) 1. Dr W. L. Straus, Jr., has called our attention to the radix communis in a specimen of the common marmoset (*Callithrix jacchus*).

Pattern C

The prevailing mammalian arrangement of aortic stems is that of pattern C, characterised by the truncus communis for anonyma and carotis communis

sinistra (figs. 1 C and 6). The truncus communis of our human specimens has an average length of less than 1 cm., and an exceptional length of 2·5 cm.

Incidence of pattern C: 6 *whites* (5·4 ± 2·15 per cent.) (males: 4 adults; females: 1 adult, 1 infant); 21 *negroes* (10·3 ± 2·12 per cent.) (males: 11 adults, 2 infants; females: 6 adults, 2 infants). Report I (1923) 2 negroes (2·3 per cent.).

Among the very large number of Mammals in which this pattern occurs, the truncus communis is as a rule relatively much longer than in Man, and there is wide diversity as to the placement of its branches. In some Mammals the subclavia dextra is the first branch given off, the truncus continuing as a further common stem for the carotides. Among our material this latter arrangement is found in the following: *Felis domestica* 10, dog (*Canis familiaris*) 1, Siberian tiger (*Felis tigris*) 1, green guenon (*Lasiopyga callitrichus*) 1, bonnet macaque (*Pithecus sinicus*) 1. In most of our specimens the truncus communis approaches that found in man by giving off the carotis communis sinistra as the first branch. This arrangement is found in the following: *Felis domestica* 24, *Canis familiaris* 2, orang-utan (*Pongo pygmaeus*) 1, gibbon (*Hylobates leucogenys*) 1, *Pithecus rhesus* 9, *P. sinicus* 6, Javan macaque (*P. mordax*) 2, common macaque (*P. irus*) 2, *Ateles ater* 3, *Lasiopyga callitrichus* 6, sooty mangabey (*Cercocebus aethiops*) 1. From Dr Straus we have records of this type of truncus communis in the following: slow loris (*Nycticebus borneanus*) 1, *Ateles geoffroyi* 1, *Pithecus rhesus* 1. In certain cases (*Felis domestica* 5, *Canis familiaris* 2) there is precise trichotomy of the truncus communis.

Combined incidence of patterns B and C

Since, as already mentioned, pattern B is not accounted separately in the literature, it is necessary to combine the frequencies of patterns B and C in order to make an approximate comparison with the findings of other authors. Therefore it must be borne in mind that the figures here cited per centum from the literature are those given by the respective authors for frequency of the so-called common trunk. These figures are as follows: English—Quain (1844) 11·8, Thomson (1893) 10·2; Japanese—Adachi (1928) 10·9; American White—Report I (1923, amended) (patterns B and C) 7·7, present report 13·5; American Negro—Report I (1923) 13·5, present report 35·4. The frequencies here given from the present report do not include certain other variants with which pattern B or pattern C is associated.

Pattern D

The distinctive feature of pattern D is the origin of the vertebralis sinistra from the aortic arch between carotis communis sinistra and subclavia sinistra (figs. 1 D and 12). Among the 8 specimens in which this anomaly occurs, the vertebralis sinistra begins its vertebral course at the foramen transversarium of the following cervical vertebrae: fifth in 3 cases, sixth in 4 cases, seventh

in 1 case. In two negroes (male, female) pattern D is associated with the truncus communis (pattern C). In the male specimen with truncus communis, the vertebralis sinistra arises ventral to the subclavia sinistra, this latter being closely crowded against the truncus communis. In other cases of pattern D the vertebralis sinistra emerges from the arch in a plane somewhat dorsal to one or both left stems (see fig. 12).

Incidence of pattern D: 2 *whites* (male adults) (1·8 ± 1·26 per cent.); 6 *negroes* (5 male adults, 1 female infant) (2·9 ± 1·17 per cent.).

Incidence of pattern D from the literature, per centum: English—Thomson (1893) 5·8; Italian—Pellegrini (1906) 5·7; Japanese—Adachi (1928) 4·8; Indian—Iyer (1928, Madras, 828 subjects) 0·8; American Negro—Bean (1905) 5·2, Report I (1923) 1·1; American White—Report I (1923) 1·9.

Pattern D^1

Intermediate between the aortic vertebralis sinistra (pattern D) and the normal is the arrangement (pattern D^1, not figured) in which the vertebralis sinistra arises from the subclavia sinistra very near the aortic arch. In both of our specimens having this arrangement the origin of the vertebralis sinistra is less than 1 cm. from the aorta; also in both the artery in question begins its vertebral course at the foramen transversarium of the fifth cervical vertebra.

Incidence of pattern D^1: 1 *white* (male adult) (0·9 ± 0·90 per cent.); 1 *negro* (male adult) (0·49 ± 0·49 per cent.).

Pattern E

This pattern of the anomalous subclavia (figs. 1 E and 7)* includes three slightly different arrangements of aortic stems, all arrangements, however, being characterised by the subclavia dextra arising dorsally as the last branch from the left extremity of the aortic arch. In two cases (negro males) there are four separate stems from the arch, the right-to-left sequence being: carotis dextra—carotis sinistra—subclavia sinistra—subclavia dextra. In two cases (negro females) this sequence is varied by a common trunk for carotides. In one case (negro male) the carotides and subclavia sinistra are closely crowded and arise by a common root.

Four of these cases have been completely dissected by two of us (I. B. and E. R.), and the following relations are demonstrated: in each case the anomalous subclavia dextra passes between the oesophagus and vertebral column; the vertebralis dextra is retained as a subclavian branch; the ansa

* Fig. 1 E serves to indicate relations to the trachea and oesophagus, but is necessarily diagrammatic. In none of the specimens reported here can the origin of the anomalous subclavia be seen from in front, since it arises dorsally from the left extremity of the arch, not from the descending aorta, as represented in fig. 1. The specimen photographed from behind (fig. 7) shows the typical arrangement.

subclavia of the truncus sympatheticus is robust; the ductus thoracicus empties into the angulus venosus of the left side; there is no nervus recurrens on the right side. In one specimen the nervus laryngeus inferior on the right side, though not recurrent in relation to neighbouring structures, is distinctly curved downward in its course to the larynx; in another specimen this nerve is recurrent under the thyreoidea inferior; in two specimens the nerve passes directly to the larynx.

A recent specimen of pattern E, not dissected under our supervision, was removed with heart and lungs, so that no information is available as to the thoracic relations of the anomalous subclavia, save that it passed behind the oesophagus. The complete aortic pattern was kindly added to our collection, and the following branches of the anomalous subclavia have been identified: vertebralis, mammaria interna, truncus thyreocervicalis.

Incidence of pattern E: 5 negroes (2·46 ± 1·08 per cent.) (3 male adults, 2 female adults).

In reference to the anomalous subclavia dextra from Report I it may be recalled that the vertebralis on the right side arose, not from the subclavia, but from the carotis communis dextra, thus involving a somewhat different interpretation than that applying to the cases here. Interpretations of the anomalous subclavia dextra have received much attention in the literature. Cairney (1925) has ably discussed this subject, especially in the light of recent work on the development of the aortic arches by Congdon (1922). The interpretation of the anomalous subclavia from Report I has been discussed in connection with an anomalous pattern of arm arteries on the right side (De Garis, 1932). One of the cases reported by Adachi (1928) was likewise associated with anomalies of the arm arteries. Among the five cases reported here, four are known to have no gross anomalies of the arteries in the upper arm. One of these four had in each forearm a large mediana which passed deep to the transverse carpal ligament and terminated in the arcus volaris superficialis. Regarding the arm arteries of the fifth case we have no information.

The high incidence of the anomalous subclavia dextra (pattern E) in negroes as compared to other races is shown in the following enumeration per centum from the literature: European—Quain (1844) 0·4, Tiedemann (1846) 0·8, Turner (1862) 0·4, Thomson (1863) 0·6, Thomson (1893) 1·0, Leboucq (1894) 0·5, Stieda (1894) 0·8, Götz (1896) 0·8, Holzapfel (1899) 0·6; Japanese—Adachi (1928) 0·2? or 0·38; Negro—Loth (1912) 9·7*; American Negro—Bean (1905) 3·5, Report I (1923) 1·15, present report 2·46.

The anomalous subclavia dextra has very seldom been encountered in other Mammals. Cuvier (1810) refers to it as having been found in the hedge-

* Loth's very high incidence of the anomalous subclavia in negroes serves to illustrate, as does the high incidence of the aortic thyreoidea ima in Report I, the statistical distortion resulting from a large distribution of one type within a small group. Within a group of 31 negro specimens he found the anomalous subclavia 3 times.

hog; Ogilvie and Cathcart (1874) found it in the lamb; Smith (1891) found it in the rabbit.

Pattern F

In this pattern the thyreoidea ima arises from the arch of the aorta between anonyma and carotis communis sinistra. In one of our specimens (negro male) the artery is extremely slender and passes in a tortuous manner to the left lobe of the thyroid gland, the thyreoidea inferior on the left side being normal in origin and course and only slightly smaller than its fellow of the opposite side. In our other specimen (negro female) the thyreoidea ima (fig. 1 F) is distributed symmetrically by medial branches to the infrahyoid muscles and trachea and by lateral branches to the thyroid gland. On each side the thyreoidea inferior is normal in origin and course, but is much reduced in size. In neither of our specimens does the thyroid gland appear enlarged.

Incidence of pattern F: 2 *negroes*, male and female adults (0·98 ± 0·69 per cent.).

Incidence of pattern F from the literature, per centum: Russian—Gruber (1872) 0·5; English—Thomson (1893) 0·4; Italian—Livini (1900) 1·0; Japanese—Adachi (1928) 0·36; American White—Report I (1923) 3·8; American Negro—Report I (1923) 4·6. The high incidence of pattern F in Report I is surely not a typical distribution for either race (see p. 606, n.).

Pattern F^1

In this pattern the thyreoidea ima is given off by the anonyma, at times from its distal third (here 2 cases), at times from its proximal third (here 3 cases), usually from its intermediate third. In one of our cases (negro male) the thyreoidea ima supplies only the left lobe of the gland and the thyreoidea inferior on the left side is lacking. In one case (white female) the thyreoidea ima is very slender and supplies only the right lobe, the thyreoidea inferior on that side not being appreciably reduced. The only case of the thyreoidea ima associated with marked enlargement of the gland is in a male white; in this case the artery is very robust, the thyreoidea inferior on the left side is absent and the other arteries to the gland are enlarged. In two cases (male and female negroes) the thyreoidea ima is associated with, but does not exclusively supply, a pyramidal lobe of the gland.

In one case (negro female) the thyreoidea ima is associated with the truncus communis (pattern C) and arises from the anonyma very near its proximal end; in two cases (white male, negro male) it is associated with the radix communis (pattern B) and arises from the middle third of the anonyma. In one case (negro female, fig. 9) patterns F^1 and H are combined, there being a short anonyma sinistra and a long anonyma dextra, the latter near its bifurcation giving off the thyreoidea ima. This case is included in the statement of incidence for each pattern, but is entered separately in Table I as F^{1}H.

Incidence of pattern F[1]*: 4 whites* (3·6 ± 1·77 per cent.) (males: 3 adults; females: 1 adult); 7 *negroes* (3·4 ± 1·27 per cent.) (males: 3 adults, 1 infant; females: 2 adults, 1 infant).

Incidence of pattern F[1] from the literature, per centum: English—Quain (1844) 3·2; Russian—Gruber (1872) 10·5; Swiss—Streckeisen (1886) 10·0; Italian—Livini (1900) 4·0; Japanese—Adachi (1928) 7·8; American Negro—Bean (1905) 4·3; Report I (1923) 4·6; American White: Report I (1923) 1·9.

The current text-book statement that the thyreoidea ima occurs in about 10 per cent. of cases is perhaps traceable to the figure of Gruber cited above. Considering collectively the various types of the thyreoidea ima for all nationalities and races in which it has been observed, a figure between 5 and 6 per cent. would appear to be nearer the true average frequency.

Occasionally the thyreoidea ima is recorded as arising from the carotis communis dextra. We have found this arrangement at a high cervical level in the dog (1 specimen), but have not encountered it in our human material; Gruber and Livini likewise did not find it; Streckeisen and Adachi each found it twice.

In our mammalian material no example of the thyreoidea ima has thus far been found, except in the dog, mentioned above, and in the chimpanzee. Among four specimens of aorta from chimpanzee, the thyreoidea ima arises from the root of the carotis communis sinistra within 1–2 mm. of the arch in two cases, from a short left truncus communis (anonyma sinistra) in one case, and is lacking in one case. Concerning the thyreoidea ima in primates Keith (1895, p. 455) remarks that this artery arises from the aortic arch in 1 chimpanzee (of 11 examined), and from the carotis communis sinistra in 1 gorilla, 4 gibbons, 3 semnopitheques, and 2 macaques; in the last two genera it is a branch of the carotis in the neck region.

Pattern G

In this singular pattern (fig. 1 G) an artery, having the terminal distribution of the thyreoidea ima or inferior, emerges as a sizable trunk from the upper part of the descending aorta and passes upward in the interval between trachea and oesophagus, distributing twigs to these two structures. Just above the convexity of the aortic arch it turns sharply to the ventral aspect of the trachea, supplies twigs to the infrahyoid muscles and trachea, and terminates on the deep surface of the thyroid gland, sending branches to each lobe. The other thyroid arteries are normal in origin and course, though both inferior arteries are reduced. Our one example of this pattern also includes the radix communis (pattern B).

There appears to be no precedent for the anomalous thyreoid artery of pattern G. It may be significant that in this specimen there are only two bronchial arteries, the first right aortic intercostal artery supplying the right bronchial, the left bronchial arising from the aorta just above the anomalous

thyroid artery. If this anomalous artery be regarded as an aberrant bronchial stem, then it is one with tracheal, oesophageal and thyroid connections, but no bronchial distribution whatsoever.

Szawlowski (1888) has reported a case of anomalous vertebralis dextra which had an origin from the aorta practically identical with that of our anomalous thyreoidea. Such a case is explained by Kemmetmüller (1911, fig. 16) as persistence of the junctional part of the right dorsal aorta plus a postcostal longitudinal anastomosis. If the anomalous thyreoidea of pattern G be regarded as the junctional portion of the right dorsal aorta, the interruption must have occurred in the plane of the oesophagus and trachea, leaving the original stem with only tracheal, oesophageal and thyreoid anastomoses. This is the explanation which we favour, though we are bound to admit that the adult condition does not warrant any fast conclusion.

Incidence of pattern G: 1 *negro* male adult (0·49 ± 0·49 per cent.).

Pattern H

In this pattern (fig. 1 H) there is a bi-anonymous sequence, the anonyma of each side giving rise to carotis communis and subclavia. Also in one specimen (previously noted, fig. 9) the anonyma dextra gives off the thyreoidea ima. In the specimen of fig. 9 the anonyma sinistra is scarcely 1 cm. long; in the specimen of fig. 1 H the anonyma sinistra measures roughly 2 cm., the anonyma dextra 3 cm.

Pattern H has been figured by early commentators from occasional human records. Tiedemann (1822) regards the bi-anonymous arrangement as most frequent in Mammals with short necks. He found it in the bat, and cites Daubenton as finding it in *Pteropus rufus*, also Cuvier as finding it in the porpoise. Parsons (1902) likewise found this arrangement in the Cheiroptera (3 species), and in two species of mole, in the hedgehog, and in certain Cetacea. In our mammalian material the sequence of pattern H occurs but once, this being from a recent specimen of chimpanzee. Here the anonyma sinistra, though less than 0·5 cm. long, is a distinct truncus communis for carotis communis sinistra and subclavia sinistra; about 2 mm. from the aorta it gives off the thyreoidea ima.

Incidence of pattern H: 2 *negroes* (0·98 ± 0·69 per cent.) (adult male and female). There is a duplication here of one specimen also included under the incidence of pattern F^1. This specimen is accounted separately in Table I as F^1H.

Pattern H^1

This pattern (fig. 8) is characterised by a radix communis for the carotis communis sinistra and subclavia sinistra. Such an arrangement is the expected intermediate between the bi-anonymous pattern H and the type of normal pattern wherein the two left stems, though distinctly separate, arise close together and usually at an interval from the anonyma. When the left stems

are thus closely crowded, their fascial coverings often render it difficult to ascertain whether they are completely separate in origin or not. However, if the aortic arch be laid open and the exits viewed from the smooth interior, the question as to separate or common origin may be answered unequivocally.

Incidence of pattern H[1]*:* 2 *whites*, male adults (1·8 ± 1·26 per cent.); 8 *negroes* (3·94 ± 1·36 per cent.) (males: 5 adults; females: 2 adults, 1 infant).

Pattern I

This pattern (fig. 11) is peculiar in having the truncus communis for anonyma and carotis communis sinistra and the radix communis for the truncus and the subclavia sinistra. This completely clumped arrangement is the logical extreme of the tendency toward crowding and fusion of the great stems, and for that reason might be expected to occur with some degree of frequency. Yet in our human material we have found it elsewhere only in the combined pattern IJ. In both patterns I and IJ the aortic arch is of very high pitch.

Among our mammalian material the completely clumped pattern I is found in the following: domestic cat 2, dog 1, *Ateles ater* 1, *Perodicticus potto* 1. In these the subclavia sinistra arises at the root of a long truncus communis for subclavia dextra, carotis communis dextra and carotis communis sinistra.

The completely clumped arrangement of the great aortic stems in Man is a clear intimation of the candelabrum, or single aortic stem, which according to Tiedemann (1822) is found especially in Mammals with long necks. Parsons (1902) figures exceptional cases of the Carnivora and Rodentia and a considerable number of the Ungulata as having one or another variety of the single stem, yet curiously enough, in the light of Tiedemann's generalisation, the giraffe and llama are found to have the subclavia sinistra widely separate from the truncus communis of the other stems. Recently we have acquired a specimen of aortic arch from the musk ox (*Ovibos m. wardi*) where the single aortic stem is a conspicuous feature.

Incidence of pattern I: 1 *negro*, male adult (0·49 ± 0·49 per cent.). The true incidence of the common origin for all great aortic stems requires the inclusion of pattern IJ, thus giving a total of 2 negroes (0·98 ± 0·69 per cent.). This entry is not duplicated in Table I.

Pattern J

This pattern (fig. 10; see also fig. 1 IJ) is peculiar in that the vertebralis sinistra arises as the last branch of the aortic arch, i.e. to the left of the subclavia sinistra. In the specimen of fig. 10 the vertebralis sinistra is in series with the intercostales, and enters the foramen transversarium of the seventh cervical vertebra.

This anomaly is apparently rare among whites and negroes; in truth for negroes we find no previous record of it whatsoever. Among whites it was

seen twice by Tiedemann (1822, Table III, figs. 1 and 10), who also cites cases from Walter, Winslow, and Meckel. However, neither Quain nor Thomson found a single instance of this anomaly in their extensive material (a total of 800 specimens). Adachi (1928) reports 3 cases among 516 specimens of Japanese (0·6 per cent.).

Incidence of pattern J: 1 *negro*, female adult (0·49 ± 0·49 per cent.). The true incidence of this anomalous vertebralis sinistra requires the inclusion of pattern IJ, thus giving a total of 2 negroes (0·98 ± 0·69 per cent.). This entry is not duplicated in Table I.

Pattern IJ

This combination of anomalies (fig. 1 IJ) has, as in pattern I, the truncus communis—radix communis for all great stems of the aorta, and, as in pattern J, the vertebralis sinistra arising as the last branch of the aortic arch. The vertebralis sinistris in this case, as in pattern J, is in series with the intercostales and enters the foramen transversarium of the seventh cervical vertebra.

This combination of anomalies has not, as far as we know, been previously reported.

Incidence of pattern IJ: 1 *negro*, male adult (0·49 ± 0·49 per cent.).

Pattern K

This pattern (not figured) is one of the right aorta, the arch and stems being a mirror-image of the normal, i.e. the sequence from *left* to *right* is: (1) anonyma, giving rise to subclavia sinistra and carotis communis sinistra; (2) carotis communis dextra; (3) subclavia dextra. This case has been fully described and figured by Sprong and Cutler (1930). Their report should be consulted for details of the case and for a most comprehensive treatment of the literature.

Incidence of pattern K: 1 *white*, male adult (0·9 ± 0·9 per cent.).

THE EXTENT AND CHARACTER OF AORTIC VARIATIONS IN AMERICAN WHITE AND NEGRO STOCKS

In Table I is given a summary of aortic patterns as they occur in the white and negro specimens of our series. The most striking feature of this table is the greater number of diverse patterns represented in the negro group. Pattern A being normal (most frequent) in both groups, the number of cases in each group having patterns outside the normal would express the extent of variability. Thus there are in whites 25 cases outside the normal (22·6 ± 3·97 per cent.), in negroes 106 (52·3 ± 3·50 per cent.). While the difference in number of variants is here so large as to appear at once significant, it is possible to express this significance numerically, the tested variants in this

instance being the total variants in whites and negroes respectively*. In this comparison the value of the constant χ^2 is found to be 26, from which the interpolated value of P is 0·0000004. In other words we would expect to get an equal or greater value of χ^2 on random sampling 4 times in 10,000,000 trials. We may therefore regard the above findings in whites and negroes as being in a very high degree significant.

As for variability according to sex within the two races, the female whites numbering 13 (5 adults, 8 infants) are, like the infants of both races (11 whites, 22 negroes), too few to be accounted as separate statistical groups. There is,

Table I. *Summarising the incidence of aortic patterns in white and negro stocks*

	Whites 111 specimens		Negroes 203 specimens	
Patterns	Samples	%	Samples	%
A	86	77·4 ±3·97	97	47·70 ±3·50
B	9	8·1 ±2·59	51	25·10 ±3·03
C	6	5·4 ±2·15	21	10·30 ±2·12
D	2	1·8 ±1·26	6	2·90 ±1·17
D^1	1	0·9 ±0·90	1	0·49 ±0·49
E	—	—	5	2·46 ±1·08
F	—	—	2	0·98 ±0·69
F^1	4	3·6 ±1·77	6	2·90 ±1·17
F^1H	—	—	1	0·49 ±0·49
G	—	—	1	0·49 ±0·49
H	—	—	1	0·49 ±0·49
H^1	2	1·8 ±1·26	8	3·94 ±1·36
I	—	—	1	0·49 ±0·49
J	—	—	1	0·49 ±0·49
IJ	—	—	1	0·49 ±0·49
K	1	0·9 ±0·90	—	—

it may be noted, a comparatively large distribution of variants among these small groups, involving mainly the patterns B and C. The female negroes numbering 65 (56 adults, 9 infants) show slightly more distribution of variants than do the negro males numbering 138 (125 adults, 13 infants): thus variants in female negroes 37/65 or 56·9 ± 6·17 per cent.; variants in male negroes 69/138 or 50·0 ± 4·27 per cent. It would be a matter of interest to work with equally representative numbers of males and females among the two races in order to find out how variations are distributed according to sex. This enterprise, however, is not feasible, since the supply of laboratory material is usually much limited as to female subjects.

* The test of significance (goodness of fit) depends on the value of χ^2 according to the following equation, adapted from its more general form for present purposes:

$$\chi^2 = \frac{(n_1.d_2 - n_2.d_1)^2.(N_1 + N_2)}{N_1.N_2.(n_1 + n_2).(d_1 + d_2)},$$

where N_1 is the total number of negroes; N_2 the total number of whites; n_1 the number of the observed variant in negroes; n_2 the number of the observed variant in whites; d_1 all other negroes examined, i.e. $N_1 - n_1$; d_2 all other whites examined, i.e. $N_2 - n_2$. The expression for probability (P) is found by turning up the value of χ^2 from interpolation in Table XV (C), p. 30, *Tables for Statisticians and Biometricians*, edited by Karl Pearson, Cambridge, 1914.

In Report I (1923), where the two groups are less than half as large as those dealt with here, the greater variability of the aortic branches in negroes is also striking: thus, including the amendments already noted, variants in whites 8/52 or 15·3 ± 4·97 per cent., variants in negroes 23/87 or 26·4 ± 4·72 per cent. The same tendency toward greater variability of arterial patterns in negroes is a conspicuous result of work on the arm arteries. The records thus far reported are on the subclavian artery (De Garis, 1924) and the axillary artery (De Garis and Swartley, 1928).

On the basis of the present report it may be inquired whether or not any variant patterns of the aortic stems occur with sufficient frequency to warrant the assumption that such patterns constitute, for one group or the other, a racial tendency. Without for the moment attempting to define the "sufficient frequency" involved in this question, it is at least possible to discuss certain preponderancies which seem significant. Among the whites there is obviously no variant pattern requiring attention here. Among the negroes there are two groups of patterns which should be considered, namely (1) the partial or complete mammalian patterns B and C of the radix communis and truncus communis, and (2) pattern E of the anomalous subclavia dextra.

Concerning the frequency of the first group of patterns (B and C) in negroes, there is a statement by Keith (1895) to the effect that the common trunk for anonyma and carotis communis sinistra occurs three times as often in negroes as in whites. For our material the combined frequencies of patterns B and C in negroes and whites respectively are as follows: negroes 35·4 ± 3·35 per cent., whites 13·5 ± 3·23 per cent. While this falls somewhat short of the 3:1 ratio mentioned by Keith, it is interesting to apply the test of significance here. With patterns B and C occurring in negroes 72/203 and in whites 15/111, the value of the constant χ^2 (see p. 612, n.) is found to be 19·7, whence the interpolated value of P is 0·0000089; that is, we should expect to get an equal or greater value of χ^2 in random sampling 89 times in 10,000,000 trials. This, indeed, indicates a high degree of significance.

In connection with patterns B and C it is a matter of further interest to canvass all the other variant patterns for cases in which there is any degree of union between the origins of the anonyma and carotis communis sinistra. Among cases of pattern D there are two having the truncus communis (negroes); among cases of pattern F^1 there are two having the radix communis (1 white, 1 negro), and one having the truncus communis (negro). The exceptional pattern G of the thyreoidea includes also the radix communis (negro). A further negro case may be added from pattern I and another from pattern IJ, since one peculiarity of these patterns is the extreme clumping of all the great aortic stems. With the foregoing cases included, the combined frequencies of radix communis and truncus communis are as follows: negroes 79/203 or 38·9 ± 3·42 per cent.; whites 16/111 or 14·4 ± 3·33 per cent. From this over-all incidence it is found that patterns B and C occur among negroes and whites in the ratio 2·7:1. The combined frequencies of the same patterns

in Report I (amended) are: negroes 12/87 or 13·8 ± 3·69 per cent.; whites 4/52 or 7·9 ± 3·74 per cent. Here the ratio is 1·7:1.

From these comparisons it is seen that while our ratios are nowhere quite as large as that suggested by Keith, there is in both present and previous reports a large preponderance of negroes over whites having the partial or complete mammalian pattern of aortic stems. Not only does this preponderance contribute much to the net result of greater variability in negroes than in whites, but also on a statistical basis it must be taken to mean that the prevailing mammalian pattern is, in truth, a racial tendency among negroes[1].

Regarding the anomalous subclavia dextra (pattern E), the very high incidence of this in negroes as compared to whites has already been shown in the tabulation from the literature. To reach an over-all incidence of this anomaly in the two races the following reports are used: *whites*—Quain (1844) 1/212, Thomson (1893) 5/500, Report I (1923) 0/52, present report 0/111, total 6/875 or 0·68 ± 0·26 per cent.; *negroes*—Giacomini (1882) 2/8, Bean (1904) 2/57, Loth 3/31, Report I (1923) 1/87, present report 5/203, total 13/386 or 3·36 ± 0·76 per cent. Testing these totals for significance (see p. 612, n.) the value of the constant χ^2 is found to be 12·9, whence the interpolated value of P is 0·00031, i.e. we would expect an equal or greater value of χ^2 in random sampling 31 times in 100,000 trials. While the test here is not as decisive as it has been for other distributions among the two races, it is still a figure of high order as indicating significance. Pending further data, we are much inclined to regard this anomaly as a true racial tendency among negroes*.

Concerning racial variants of the aortic arch, Vallois (1929, p. 91) remarks: "La seule variation raciale incontestable que l'on puisse noter est la plus grande frequence du type III chez les Noir...," wherein type III (his fig. 6) can only be interpreted as the right-to-left sequence: subclavia dextra—carotis communis dextra—carotis communis sinistra—subclavia sinistra, each arising separately from the aortic arch (see here p. 602, n.). In support of his assertion, he says Loth (1912) reports type III in 9·7 per cent. of negroes, whereas Thomson (1893) reports the same type in but 1 per cent. of whites. Essentially the same statement is taken over by Weinert (1932). Now it is truly astonishing to find that neither Loth nor Thomson has ever reported such an arrangement as that of Vallois's type III. However, the per centum figures cited by him are exactly those of the respective frequencies found by Loth and Thomson for the anomalous subclavia dextra arising from the left extremity of the aortic arch (here pattern E). Thus it seems apparent that through some misapprehension Vallois, followed by Weinert, has figured a rare aortic anomaly as one of the incontestable racial variations in negroes, whereas, tracing his statement to its factual sources, we find that he has,

* Williams (1932) has found that the common origin of anonyma and carotis communis sinistra is much more frequent in negroes than in whites. Also he announces a high incidence of the anomalous subclavia dextra in negroes.

however inadvertently, said what we are saying in the present report, namely that the anomalous subclavia dextra is a true racial variation in negroes.

Concerning the material here spoken of as negro, it is well to recall that the American negro population is customarily regarded as mixed, to some extent with American Indian stock, to a much larger extent with white stock. The bearing of this race mixture on the question of greater variability among negroes has been discussed in a previous report (De Garis and Swartley, 1928). In the recent work of Loth (1931) there are valuable collections of data on the soft parts of various races, including negroes other than American. However, his chapter on the vascular system, in so far as it deals with the negro, cites data largely drawn from American sources. Nor is there any large series of other negro material available for comparison with our present findings.

In this connection the points we wish to emphasise are these: we do not really know what is the normal aortic pattern for other or so-called pure negro stocks (if such exist); nor do we know the range of variability in these stocks. From present findings we have assumed that the normal for negroes is the same as that for whites. But our further finding of greater variability in negroes is open to several interpretations: (1) since range of variability is an obverse measurement of the normal, there may actually be more than one pattern so frequent in negroes as to be considered normal; or (2) there may be a true racial tendency in negroes toward more unstable vascular patterns; or (3) this instability may be due to race-crossing. The first interpretation is so bound up with the second that, it seems to us, a true estimate of variability in negroes is best served by measurement from a single normal. As for the second and third interpretations, it is manifestly impossible to separate the factors of racial variability and hybrid variability in the American negro material with which we have to deal.

In the case of certain aortic patterns, namely (1) the partial or complete mammalian patterns (radix or truncus communis for anonyma and carotis communis sinistra), and (2) the anomalous subclavia dextra, we have already indicated that their preponderance in negroes is so distinct as to warrant the assumption that they represent true racial tendencies, or in terms of hybridisation, tendencies owing their increment to negro stock.

DISCUSSION

In considering what, if any, conclusions of a general nature may be drawn from the foregoing study of aortic patterns in whites and negroes, we would at once avoid the terms *high* and *low* as designating one or another race, since not only do these terms imply an invidious comparison but also a comparison far more simple than the facts permit.

Some of the facts are these: In our present and previous studies on the vascular system of whites and negroes we have found a much greater range of variation in negroes, except for arteries at the base of the brain, where the

range of variation is reversed (these latter data unpublished). As for the muscular system, there is a general impression that negroes are more variable than whites, an impression perhaps traceable to reports by Chudzinski. Here, selecting for illustration such statements as are readily available, we find that Howell and Straus (1931) report accessory humeral heads of the biceps brachii occurring more frequently in negroes than in whites. Their further observations confirm this report (personal communication). On the other hand, Thompson, Batts and Danforth (1921) have found that the palmaris longus is more frequently absent in whites than in negroes. Again, the ilium of the negroes of both sexes, according to Straus (1927), is on the average slightly less variable than that of the whites of corresponding sex, although the stock differences are so slight that the two races "may really be regarded as having like variability in the characters examined." Also in certain measurements on living models Herskovitz (1927, 1928) found that negroes are somewhat less variable than whites, though not so in all the measurements made by him.

These few illustrations suffice to show that in a comparison of the two races we have the usual concurrence of independent variables, biologically speaking. Therefore it is meaningless to say that negroes are more variable than whites, simply because we find that much of their arterial system is more variable. In at least one part of this system they are known to be less variable; likewise in other systems or parts they are known to be less or more variable. At present, then, all we can do with this comparison is to remain at once tentative and concise, i.e. concise and very explicit as to the parts compared, and altogether tentative as to general conclusions.

Speaking now only of the aortic arch in negroes and whites, what broad concepts are exemplified here? Schultz (1926, p. 323) has said, "Evolution will continue as long as variations occur." Since this statement seems as unassailable as the fact of evolution itself, and further, since the aortic arch in negroes is clearly more variable than that in whites, it is merely syllogistic to conclude that the aortic arch is evolving more in negroes than in whites. Then what is the direction of this evolution? We have found that the prevailing mammalian type (radix communis and truncus communis) is very much more frequent in negroes than in whites. Is the aortic arch in negroes evolving toward or away from this mammalian type? If toward it, then it would seem directed toward the alleged ancestral or atavistic pattern. If away from it, then it must approach the normal and more dispersed pattern prevailing in whites. Yet this latter, according to our present conception of developmental sequence, is the more primitive ontogenetic pattern. If we accept the view of Bolk (1926, 1929) that Man is a fetalised Mammal and has become stabilised as a result of retardation, then the negro in his aortic arch is less fetalised, less stabilised, more rapidly evolving and in the direction of the mammalian type.

This exercise in logic serves at least to point the horns of the dilemma and to confirm our present diffidence toward facile generalisations. Yet to be sure,

those of us who find adventure in this work cherish the hope that we are adding facets to a large mosaic wherein the races of men will ultimately appear in their true and significant contrasts.

SUMMARY

Among 314 subjects (111 whites, 203 negroes) are found 16 different patterns of branches associated with the aortic arch. Among whites 8 of the 16 patterns are represented, among negroes 15 of the 16. The text-book sequence (anonyma, carotis communis sinistra, subclavia sinistra, as separate stems) is most frequent or normal in both races. The gross incidence of variant patterns is: in whites $22{\cdot}6 \pm 3{\cdot}97$ per cent.; in negroes $52{\cdot}3 \pm 3{\cdot}50$ per cent. Among whites no variants occur often enough to suggest a racial tendency. Among negroes two groups of variants are conspicuous: (1) the prevailing mammalian patterns (radix communis and truncus communis for anonyma and carotis communis sinistra), taken together, occur 2·7 times as often in negroes as in whites; (2) the anomalous subclavia dextra occurs exclusively in negroes (5 cases, $2{\cdot}46 \pm 1{\cdot}08$ per cent.). By statistical test the higher incidence of these two groups of variants in negroes than in whites is found to be significant. Hence it is assumed that these particular variants represent true racial tendencies among negroes, or in terms of hybridisation, tendencies owing their increment to negro stock. The general finding of large diversity in aortic patterns among negroes, though by test significant, may be a hybrid variability, or a racial variability, or both. Comparisons are made with such aortic patterns as occur in our mammalian material.

For most of our Primate material and its identification we are deeply indebted to Dr A. H. Schultz and Dr W. L. Straus, Jr., who advise the nomenclature of D. G. Elliot (*A Review of the Primates*, 1913). Recent important contributions to our collection have been made by Prof. John F. Fulton, New Haven. Certain valued specimens from the U.S. National Museum were obtained for us by Mr Brazier Howell. Two specimens of *Pithecus irus* were kindly furnished by Dr G. W. Corner, Rochester. For aid in the statistical treatment of significance we wish to thank Dr Carroll Palmer.

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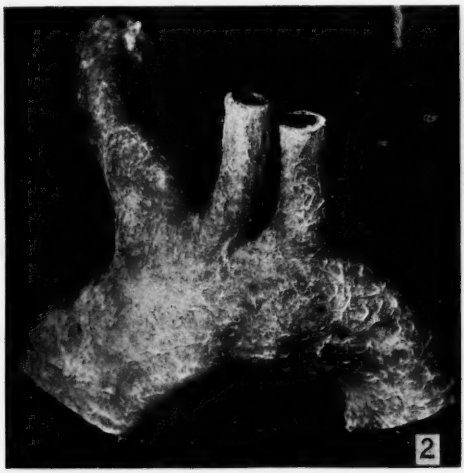
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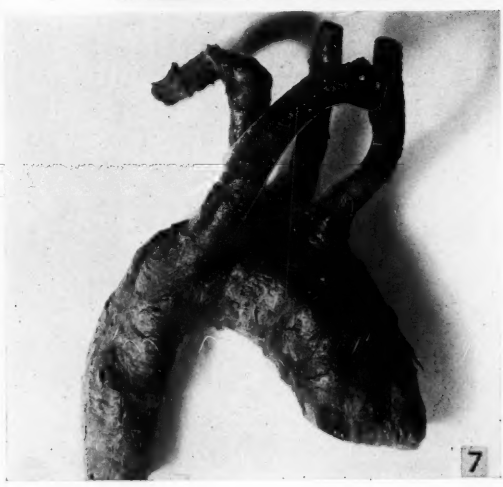
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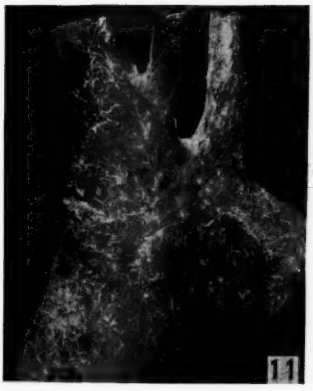
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EXPLANATION OF PLATES

PLATE I

Fig. 2. *Pattern B,* the radix communis for anonyma and carotis communis sinistra. (Adult negro male.)

Fig. 3. The specimen of fig. 2, opened along the concavity of the aortic arch and viewed from within, showing the common exit of the anonyma and carotis communis sinistra.

Fig. 4. Variety of *pattern B,* with marked crowding of the aortic stems to the right extremity of the arch, the root of the anonyma giving very oblique origin to carotis communis sinistra; behind the latter is the subclavia sinistra. The specimen is inclined somewhat to the right. (Adult negro male.)

Fig. 5. The specimen of fig. 4, viewed from within. The oblique exit of the carotis communis sinistra appears as a narrow slit.

Fig. 6. *Pattern C,* the truncus communis for anonyma and carotis communis sinistra. (Adult negro female.)

Fig. 7. *Pattern E,* viewed from behind. The subclavia dextra arises dorsally as the last branch of the aortic arch. (Adult negro male.)

PLATE II

Fig. 8. *Pattern* H^1, radix communis for carotis communis sinistra and subclavia sinistra. (Negro female, age 13.)

Fig. 9. Specimen combining features of *patterns* F^1 and *H,* the thyreoidea ima arising near the distal extremity of the anonyma, the carotis communis sinistra and subclavia sinistra arising by a short truncus communis (anonyma sinistra). (Negro female, age 15.)

Fig. 10. *Pattern J,* the vertebralis sinistra arising from the aortic arch to the left of the subclavia sinistra and entering the foramen transversarium of the seventh cervical vertebra. The artery is exposed by transection of the left sympathetic trunk and the costal elements of the cervical vertebrae and by removal of the vertebralis. (Adult negro female.)

Fig. 11. *Pattern I,* aortic arch of very high pitch, the anonyma and carotis communis sinistra arising by a truncus communis with which the subclavia sinistra forms a wide radix communis. (Adult negro male.)

Fig. 12. *Pattern D,* the vertebralis sinistra arising from the aortic arch between and behind the carotis communis sinistra and subclavia sinistra. The specimen is turned somewhat forward. (Adult negro male.)

ANATOMICAL NOTES

A NOTE ON AN ABNORMAL HEART OF *RANA TEMPORARIA*

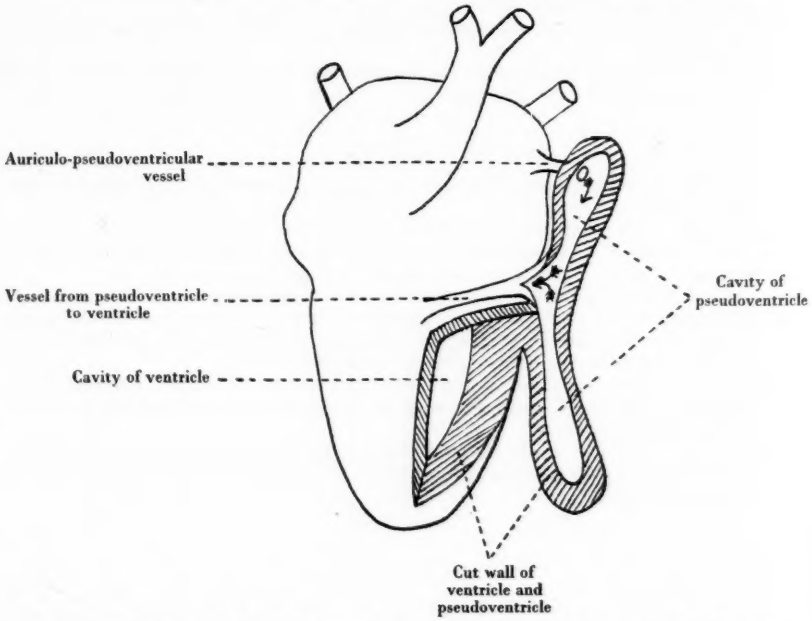
By J. R. GROOME, B.A., B.Sc. (Oxon.)

Cardiac abnormalities are commonly met with in the frog; but as these are usually confined to enlarged auricles or arterial arches, the case herewith described seems worthy of notice.

An abnormal heart was handed to me by a student, who had removed it from the animal and transferred it to 70 per cent. alcohol. It was therefore in a contracted state and inadequately fixed for microscopical examination, and so it was lightly stained, cleared, and impregnated with wax to facilitate dissection.

The animal from which this heart was removed was a male, rather above the average in size, and apparently in good condition. The heart was unusually large, and had a curious outgrowth from the left side of the ventricle. Apart from this it appeared normal, except that the cavity of the ventricle was smaller than expected.

The outgrowth was nearly as long as the heart, but only the middle portion of it



Diagrammatic drawing of abnormal heart of frog, ventral aspect. The ventricle and pseudoventricle have been opened to show the fusion of their walls. The arrows indicate the supposed direction of the blood stream.

was fused with the ventricular wall. When opened, it was found to have thick walls, with projections resembling columnae carneae jutting out into the narrow cavity. I have therefore called it a pseudoventricle. At the anterior end of this pseudoventricle was a short vessel opening into the side of the left auricle, and nearly half-way down, attached to the ventral wall of the ventricle throughout its length, was a longer vessel opening into the ventricle in the middle line. Both these vessels were very narrow with thick walls, and no traces of valves could be found.

Although it is impossible to say how this structure affected the circulation, it is probable that it was contractile. Possibly some of the arterial blood from the left auricle was transferred to the pseudoventricle, and retained there till the cavum pulmocutaneum was closed (only a small amount of blood would be treated in this way as the auriculo-ventricular valves appeared normal). Then the pseudoventricle may have contracted, driving the blood to the ventricle and thence to the cavum aorticum, thus perhaps improving the circulation by functioning as a very imperfect left ventricle.

Summary

A pseudo-ventricle is described on the left side of an otherwise normal heart. It has thick walls and projecting into its cavity are pieces of muscular tissue resembling columnae carneae.

At its anterior end is a vessel opening into the left auricle, and in the middle is a longer vessel opening into the ventricle. It is suggested that it may have functioned as a very imperfect left ventricle.

ANOMALOUS ATLANTO-OCCIPUT

By R. K. RAU, F.R.C.S., L.R.C.P. (Edin.), etc.,
and D. SIVASUBRAHMANIAM, M.R.C.S. (Eng.), L.R.C.P. (Lond.)
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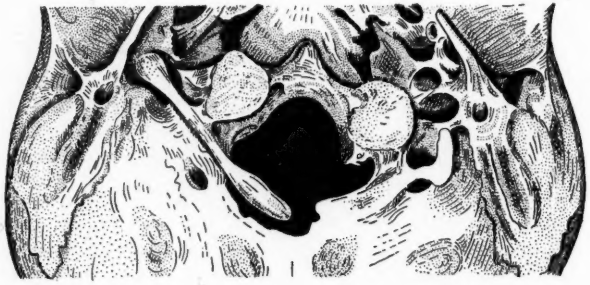
The variation described hereunder was met with in the skull of a male aged about 50 years, said to have died of cancer of the penis, in the King George Hospital, Vizagapatam, attached to this Medical College, in July, 1932.

Description

Ectocranial aspect. The skull presents normal asymmetry. The foramen magnum 35 mm. long, 33 mm. broad is situated a little further back than normal. The ventral arch of the atlas is fused with the basi-occiput. The anterior margin of the foramen magnum 15 mm. in depth is notched for the reception of the odontoid process of the axis which conforms to the normal type. The fusion has occurred in such a manner that there is a groove between the two bones on the right side, while on the left side there is none. There is an accessory foramen on the right side below and medial to the



anterior condyloid foramen between the fused atlas and the occiput and anterior to the lateral mass bearing the inferior articular process. The costal bar of the transverse process of atlas is absent on the left side, while on the right the foramen transversarium is completed in the usual manner by both the ventral and dorsal bars. The paracondyloid processes are present on both sides. They are not united to the transverse processes. The posterior arch of the atlas is deficient in the middle. The right segment of the posterior arch is distinctly separated from the occipital bone in the region of the foramen magnum by a distance of 6 mm. On its superior face, there is the usual groove for the vertebral artery and the suboccipital nerve. The bar terminates behind in a blunt rounded extremity. The left segment of the posterior arch is confluent with the squama of the occipital. There is a gap of 7 mm. to the right of the middle line between the posterior ends of the separate and fused right and left neural arches respectively. The inferior articular facets are asymmetrical and are of the atlanto-axial type. The facet on the right side is small and ovoid and measures 19 × 15 mm., while that of the left side is nearly circular and measures 18 × 19 mm. Large vascular foramina are found behind and above the inferior articular facets of both sides.

Endocranial aspect. Posterior fossa of the basis cranii interna.

The groove for the superior petrosal sinus of the left side is wider and shallower than the corresponding one of the right side.

Porus acusticus is bigger on the left side. Subarcuate fossae are well marked on both sides. Aqueducti vestibuli of both sides are indicated by conspicuous clefts. The lateral parts of the lower margins of the posterior surfaces of the pyramids of the temporals are drawn out into spines overhanging the terminal parts of the sigmoid portions of the transverse sinuses of both sides. The spines are separated from the rest of the temporals by two faint suture lines which suggest their development by independent accessory ossific centres. The anterior margin of the foramen magnum presents lateral elevations on either side of a median depression. The groove for the inferior petrosal sinus is wider and shallower on the left side. The groove for the superior sagittal sinus forks out into a right and a left groove of almost equal size. The torcular fossa is not marked though the internal occipital protuberance is well defined. The so called vermian fossa of Verga is present and is 16 mm. at the widest part. It is roughly triangular in outline with its apex at the internal occipital protuberance and its base at the posterior margin of the foramen magnum. Two ovoid depressions are found on either side of the median vermian fossa, the left being the smaller with a foramen for an emissary vein opening into it and the right the larger. There is a foramen behind the dorsal bar of the transverse process on the left side. This gives the appearance of duplication of the foramen transversarium. The left vertebral artery enters the skull directly without passing through the foramen magnum. The right artery has its usual course through the foramen magnum. On the supra-tentorial aspect there are faint ridges 30 mm. on either side of the middle line presumably for the sulci lunati.

Features of interest.

(1) Complete bilateral synostoses of the condyloid diarthroses between the occiput and the atlas.

(2) Complete concrescence of the atlas with the occiput on the left side and incomplete fusion on the right side.

(3) *Deficient* posterior arch.

(4) Apparent duplication of the vertebrarterial foramen of the left side.

(5) The presence of an accessory foramen below and medial to the anterior condyloid foramen probably for the passage of the first cervical nerve.

(6) Raised anterior margin of the foramen magnum.

(7) The presence of a wide vermian fossa.

The anomalous bones present some features indicative of the condition of "manifestation of an occipital vertebra"; others indicative of assimilation of the atlas on the left side; and finally of simple fusion on the right side.

The sketch of the specimen has been made from a drawing by our artist, Appaladas, to whom we express our thanks.

REVIEWS

Bailey's Text-Book of Histology. By A. Elwyn and O. S. Strong. 8th Edit. (London: Baillière, Tindall & Cox.) 1932. Pp. xvi + 746. 529 figs. Price 31*s.* 6*d.* net.

The present edition, which is the eighth, has been revised and rewritten by A. Elwyn and O. S. Strong in collaboration with several members of the Anatomy staff of the College of Physicians and Surgeons of Columbia University. All the contributors are engaged in teaching, and research on, histology.

In the seventh edition the chapters on the tissues and nervous system were expanded and revised. In the present edition the chapters on the organs have been revised and rewritten and a new chapter on the "Living Cell" has been added.

The book gives 700 pages of text with 529 illustrations. The spacing and margins are generous and the type clear and large. The task of the reader is thus made easy. The various chapters approach the problem of microscopic structure from the embryological side and this gives to the presentation a more intelligible and dynamic aspect. Since the full meaning of structure is only apprehended when function is understood, the physiological implications of the subject have been adequately treated.

The book is an excellent statement and exposition of the microscopic structure of the body done in such a way that the reader forgets about sections and is persuaded into believing that the things discussed are part of a living body.

The Inherited Abnormalities of the Skin and its Appendages. By E. A. Cockayne, D.M., F.R.C.P. (London: Oxford University Press.) 1933. Pp. x + 394. Price 32*s.* net.

The object of this book is to set forth the genetics of all the defects of a definite part of the body. For this purpose the abnormalities which cause changes in the skin, teeth, hair, or nails have been chosen since, whether slight or considerable, they are visible, likely to be known throughout all the family, and thus both detection and securing a pedigree are probable.

Despite the successful laboratory work on genetics, the application of the results so obtained to human affairs has on the whole been disappointing. One explanation of this lies in the paucity of the right kind of data. To correct this is one of the objects of the author. He hopes that his book will show dermatologists how deficient is our knowledge of the genetics of the defects that come under their notice. He further hopes that they will in consequence publish not only reports and pedigrees of families in which a defect is inherited but also isolated cases of the same defect. This last is important, for at the moment there is an absence of data by which to compute the ratio of the occurrence of isolated cases of a defect to the numbers of cases occurring when the same defect is handed down by direct descent in family groups. The author also makes it clear that the full family details of the isolated case are as important as for those occurring in the family groups.

The author gives his first 50 pages to a brief exposition of the chromosomal theory and a more elaborate discussion of mutations, atavism, and stigmata of degeneration of Man. He then proceeds to his groupings of abnormalities, their detection, their

pedigrees and inheritance. The author thus comments on his labours. The collection of data about the abnormalities included in the book has shown very clearly that in the case of almost all of them the information obtainable from published records is too imperfect for any definite conclusion about their mode of inheritance to be drawn and it is necessary to make a fresh start with fresh data.

The author is to be thanked for his careful and laborious work and for giving to the medical world a volume which can act as a standard work of reference for the subject he has so judiciously selected.

Kreislaufstörungen und Pathologische Histologie. Von Prof. Dr MARTIN NORDMANN. (Dresden: Theodor Steinkopff.) 1933. Pp. x + 174. Abbildungen 14. Brosch. RM. 13.80: Ganzleinen RM. 15.

This is numbered the fourth in the monographs reviewing the results of investigation of the vascular system edited by Dr Bruno Kisch, Professor of Physiology in the University of Köln.

The present monograph gives 170 pages of text and 14 illustrations with index and full bibliography. It contains a short introduction on the history of the subject and then proceeds to its task of setting forth the experiences and results which have accrued directly or indirectly from the microscopic investigation of the circulation in Man and animals during life.

The first part contains an introduction on the anatomy and physiology of tissues and their circulation. It then proceeds to methods of investigation and the discussion of capillary flow, the changes in rest and activity, constriction and dilation, hyperaemia, etc.

In the second part the fourth chapter deals with the general pathological histology of Man, its subjects being oedema, inflammation, etc. The fifth chapter is concerned with the special pathology of vascular diseases in Man, such as arteriosclerosis, endarteritis obliterans, etc.

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